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VOLUME 32 JANUARY, 1958 NUMBER 1

LATE MISSISSIPPIAN FAUNA FROM THE REDOAK HOLLOW FORMATION OF SOUTHERN OKLAHOMA

PT. 4: GASTROPODA, SCAPHOPODA, CEPHALOPODA, OSTRACODA, THORACICA, AND PROBLEMATICA

MAXIM K. ELIAS
University of Nebraska

ABSTRACT—Twenty-one species and varieties of gastropods are described, eight new; apparent relation of most forms to British Lower Carboniferous species is indicated. The genera *Retispira* Knight, *Patellilabia* Knight, *Trepospira* Girty, and *Cyclozyga* Knight are discussed and lowered in rank to subgenera. The genus *Amaurotoma* Knight is discussed, and *Pseudozygopleura* Knight is considered a junior synonym of *Zygopleura* Koken.

Five species of cephalopods are described, two new; presence of *Eumorphoceras girtyi* Elias indicates correlation with basal Namurian (E_1) of Europe.

Twenty-three species and varieties of ostracodes are described, fifteen new. Morphology of the genus *Deloia* is discussed.

The new genus *Clarkeolepis* and three new species of Thoracica are described. The problematic genus *Cyclopuncta* is introduced for scars attributed to a Fusiculina-like organism.

GASTROPODA

Genus EUPHEMITES Sowerby

EUPHEMITES COMPRESSUS, n. sp.

Pl. 1, figs. 3,4

THE new species has bellerophontid coiling and a simple sculpture, which consists of revolving costae only, so characteristic for *Euphemites* (=*Euphemus* of most authors). The form could be easily classified as a small variety of the common subglobose Pennsylvanian shell of *E. carbonarius*, if it were not for its noticeable lateral compression, the proportion of its transverse diameter to the diameter of coil being about 3:4 or 4:5. Besides smaller size and lateral compression, the new species differs from *E. carbonarius* also in proportionally wider mesial band, which is marked by the concave growth lines upon the smooth anterior of ephebic portion of the shell: the band occupies nearly $\frac{1}{3}$ of width of shell in *E. compressus*, and only $\frac{1}{5}$ or less in *E. carbonarius*. On the other hand, the lines of growth across the mesial band are not as deeply concave in the new species as in *E. carbonarius*, which all means that the sinus in the former is broader and shallower, and in the latter proportionally narrower and deeper. Diameter of adult shell in *E. compressus* is 4 mm. or slightly larger, while this diameter is up to 15 mm. in the typical *E. carbonarius* from the Wewoka of Oklahoma, and 17 mm. in the type of the species from Kentucky.

The fact that the shells of *E. carbonarius* are smaller in the Lower than in the Upper Pennsylvanian has been noticed by Mather (1915, p. 234), who found that the specimens from the Morrow are "slightly under the average size of the Coal Measures forms referred to it." The increment in size with the advance of geological age is reported by Morningstar (1922, p. 240) in *E. carbonarius* of Ohio. She finds that in the Lower Mercer and higher Pottsville horizons "it attains a much larger size than in the basal members" of the Pottsville. Her illustration of the "specimen of average size" from the Lower Mercer measures 13 mm. both in diameter of coiling and across. Girty and Roundy (1923) identified *E. carbonarius* in the Otterville and possibly Jolliff (see Tomlinson, 1929, p. 75–76) of the Ardmore Basin; it is possible that the form thus identified by them will prove intermediate between *E. compressus* and *E. carbonarius*.

The recently described *Euphemites incarinatus* from the Pitkin of Arkansas (Easton, 1943, p. 150, pl. 24, fig. 22) differs from both *E. compressus* and *E. carbonarius* by a much larger number (to 40 or more in the last whorl) of finer revolving coastae, the presence of growth lines traversing the costae, the absence of the smooth ephebic part of shell, and the absence of excavation of the umbilicus. It is peculiar that the Lower Carboniferous *Euphemites urii* of Scotland (Weir, 1931, pl. 9, figs. 3a–c and 5; Knight, 1941, pl. 12, figs. 5b–3) is nearer to our Pennsylvanian forms here discussed than the *E. incarinatus* from the Pitkin. The resemblance of *E. urii* to *E. carbonarius* is so close that some American paleontologists believed in their possible specific identity. The new illustrations of the Scotish species by Weir (reproduced by Knight) compare well in all respects with those of the specimens from the Wewoka (Girty, 1915, pl. 21, figs. 1–3), but not with *E. compressus* of the Redoak Hollow. King (1940, p. 150–151) restores McChesney's name *E. vittatus* for shells of *E. carbonarius*, as he suppresses the latter name, because given to a species "invalid and unrecognizable." None of the four species of *Euphemites*, which R. H. King (1940) recognized and describes from the Pennsylvanian of Texas, is comparable to *E. compressus*, and their age is post-Morrow.

Winchell (1862) described, but did not illustrate, *Bellerophon galericulatus* from the Waverly Series of Ohio, whose "average diameter . . . " and other dimensions are not unlike those in *E. compressus*. Herrick (1888, p. 89–90, pl. 2, fig. 34; pl. 9, figs. 32a, b) quotes in full Winchell's description, adding none of his own, and illustrates it by sketches showing great variability of lateral compression of the conch. Hyde (1953) accepts Winchell's average dimensions as characteristic for *Euphemites galericulatus* (Winchell), and shows for this species (pl. 46, fig. 21) "outline constructed according to the dimensions given in Winchell's original description for purpose of comparison" with his own material from the Waverly Series which he describes and illustrates as a new species *Euphemites subglobosus* Hyde and a questionably identified "*E. nautiloides* (Winchell)?" (Winchell, 1862, has not illustrated it). Comparison of Herrick's sketches with those by Hyde indicates that Herrick referred to *E. galericulatus* Winchell what Hyde describes as *E. sublobosus* and *E. nautiloides*. It seems permissible to conclude that Winchell's "average" dimensions represent true averages from measurements of a mixture of inflated *E. subglobosus* and slender *E. nautiloides* Hyde (not necessarily Winchell). Because Winchell, Herrick, and Hyde collected their material in the same Waverly group of about the same area in Ohio, it seems hardly possible that neither Herrick nor Hyde obtained a single bellerophontid shell (now classified as *Euphemites*) with the proportion of diameter to width like the "average" in *E. galericulatus* Winchell, if such form exists. In view of this, the absence of illustration of this species, and apparent loss of Winchell's types, it would serve no useful purpose to identify the new species *E. compressus* with *E. galericulatus*, a probable mixture of two species, none of which, taken separately, is identical with this Redoak Hollow form.

Note on genus RETISPIRA Knight

1945. *Retispira*, KNIGHT, Jour. Paleontology, v. 19, p. 335–336, pl. 49, fig. 1a–c.

The genus *Retispira* was introduced for the Devonian to Permian gastropods customarily classified with the Ordovician genus *Bucanopsis*. It is differentiated from the latter "by its simple, inducturnal inner

lip and its lack of the sharp ridge on the floor of the interior of the whorl" (Knight, 1945, p. 335). However, because the internal sharp ridge has no special biological meaning more than being a mere impression of the external ridge of the underlying earlier whorl, its taxonomic significance is hardly of generic rank. As to the structure of the inducturnal (lamellar layer at and near aperture) lip it cannot be observed on average fossil material in which the aperture is usually not preserved. In view of this, *Retispira* seems to be useful for subgeneric rather than generic differentiation, for the shells sufficiently preserved to show at least one of its characteristic features mentioned by Knight. In the described *Bucanopsis reticulatus*, n. sp., there can be observed only a very faint and rounded internal ridge in the middle of the floor of its volutions, and thus it can be placed at least questionably in the subgenus *Retispira*.

BUCANOPSIS (RETISPIRA?) RETICULATA, n. sp.

Pl. 1, figs. 5–7

?1923. *Bucanopsis* aff. *meekiana*. GIRTY & ROUNDY, Bull. Am. Assoc. Petrol. Geologists, v. 7, p. 343.

?1929. *Bucanopsis* aff. *meekiana*. TOMLINSON, Okla. Geol. Survey Bull. no. 46, p. 75,76 (listed on the authority of Girty & Roundy, 1923).

Description.—Several molds of *B. reticulata* have been recovered from locality No. 1, the largest being 8 mm. wide across the axis of volutions. The following description of the sculpture is made from the external mold of this specimen, which is selected as the holotype.

The transverse lines of growth are only slightly less prominent than the longitudinal costae, and among them also are a few more prominent elevations, which are distributed at less regular intervals among the smaller costae than the more prominent longitudinal costae. The ordinary lines of growth are very fine and can be barely observed; counting only those that are clearly visible, there are about twenty lines per 1 mm. in the slit band and the area near it. The more prominent transverse elevations have a sharp distal slope and a wider proximal slope, and they occur at somewhat irregular intervals. However, they average about 6 or 7 per 1 mm. on slit band, and only 2 per 1 mm. on either side of it. These side elevations are apparently continuous with every third or fourth of the prominent slit band elevations; their proximal slopes become particularly wide and gentle, when they start to traverse the sides of the conch at the edge of the slit band. The rest of the transverse slit band elevations, though also continued on the sides of the conch, become there nearly as weak as the ordinary growth lines.

Besides the longitudinal costae and transverse lines and elevations of growth, the external surface of conch is also marked by distinct though small shallow circular depressions. These are lined along the crests of the central and two lateral costae of the slit band, being slightly more prominent on the former. They also appear on the crests of the most prominent lateral costae, but all in all these circular depressions develop only on the mature part of conch, when it grows to about 6 mm. in diameter. There are about 5 circular depressions per 2 mm. length of the crests of costae, and they are also roughly arranged in transverse rows, which are not generally located on the crests of the transverse elevations, but in most cases fall along transverse rows, though being on the crests of the longitudinal costae, as mentioned above. Lines of growth curve broadly outward, and arch on either side of the shallow, rounded slit-band; the latter is .4 mm. wide when conch is 8 mm. in diameter.

Discussion.—It seems possible that the new species *B. reticulata* is the same form which was identified as *Bucanopsis* aff. *meekiana* by Girty and Roundy among the forms collected from the Otterville limestone of locality 4062, and also from locality 4056, which Tomlinson lists as the Otterville or possibly Jolliff. The reason for the possible identity of the form from the Otterville with the new species is the latter's closer resemblance to *B. meekiana* than to any other known species of *Bucanopsis*.

The species is like *B. meekiana* (Swallow) in size, shape, and fine reticulate sculpture, which is made of nearly equally prominent longitudinal and transverse striae. However, closer examination reveals that sculpture in *B. reticulata* is considerably more complex than that in *B. meekiana*. The greatest difference is in the sculpture of the

slit band or median band. In *B. meekiana* it is marked merely by several (5 to 8) longitudinal costae of equal prominence, but in *B. reticulata* it is made of not only same kind of costae (about 10 when conch is 8 mm. wide), but there are superposed three coarser longitudinal revolving costae, transverse lines of growth, and some scattered circular depressions. Of the three longitudinal costae, that build the slit band, the central is slightly more prominent than the lateral ones, while the circular depressions are arranged in one row along the crest of each of these costae. The total width of the slit band is .4 mm., when conch is 8 mm. wide.

The sculpture on the sides of *B. reticulata* is also finer and more complex than the same in *B. meekiana*. According to Girty the latter species has 12 to 16 subequal or "alternating" revolving costae per 3 mm. on each side of the slit band (Girty, 1915, p. 170; see also his 4 times magnified figure 6 on pl. 20), while *B. reticulata* has from 12 to 14 costae per 1 mm., that is their number is about three times larger per same space. Besides, these costae are never subequal, but every third or fourth of them is considerably more prominent than the others. The total number of these prominent costae is about 20 on each side of a conch. The intersections of the most prominent revolving and transverse costae are slightly, but nevertheless distinctly and sharply elevated.

Bucanopsis waverlianus Hyde from the Byer member, Logan formation, Waverly Series (1953, pl. 46, figs. 29–31) is undoubtedly closely related to *B. reticulata*. It has a similar umbilicus, but its sculpture, as shown in the drawings consists of very regular squares made by subequal revolving longitudinal and transverse striae, each traversed "by 1 to 5 of the finer revolving striae" (1953, p. 321), also shown in the drawings. Perhaps the regularity of the sculpture was exaggerated in the drawings, and is more nearly as in *B. reticulata*, but in view of its much younger age it is probably not identical with *B. waverlianus*. Provisionally its difference from the Waverlian form may be formulated thus: main revolving striae of diverse strength resulting in diversity of rectangles formed by crossing transverse striae, subequal in strength but irregular in spacing (pl. 30, fig. 5).

Bucanopsis textilis (Hall) from the Spergen and earlier Mississippian of America shows great similarity to *B. reticulata* in size, shape, and sculpture, in as far as can be judged from the drawings of this species by Whitfield (1882, pl. 8, figs. 4,5; 1883, pl. 31, figs. 4,5, same as in 1882; Walcott, 1884, pl. 18, fig. 18; and Cumings, 1906, pl. 25, figs. 4,5, which are reprinted from Whitfield's illustrations). The range of its size is given from $\frac{1}{8}$ to $\frac{3}{4}$ of an inch in length, and the length of *B. reticulata* falls within it. Ulrich and Scofield (1872, p. 924) remark that "in *Bucanopsis textilis* Hall (not De Koninck sp.), of the Warsaw or St. Louis group, the slit-band seems always to be without revolving lines, but in an undescribed form recurring in the Chester group of Kentucky, and which can scarcely be distinguished, such lines are clearly present." From this point of view this Chester form (still undescribed) is perhaps conspecific with *B. reticulata* from the Redoak Hollow, where the slit-band is traversed by several fairly conspicuous revolving costae (see pl. 30, fig. 5, right side). Besides the presence of these costae in the slit-band, *B. reticulata* differs from *B. textilis* also in having fairly wide umbilicus (see pl. 1, fig. 7), while in the latter "umbilicus [is] small in young shells and scarcely visible in the older specimens from the thickening of the lip" (Cumings, 1906, p. 1362, quoted from Whitfield). Apparently *B. reticulata* evolved from *B. textilis* or *B. waverlianus*, and in turn gave rise to *B. meekiana*.

Note on genus PATELLILABIA Knight

1945. *Patellilabia*, KNIGHT, Jour. Paleontology, v. 19, p. 336–388, pl. 49, fig. 3a–f.

In his revision of Paleozoic gastropod genotypes, Knight pointed out the unsatisfactory preservation of *Bellerophon macrostoma* Roemer (which is the generotype of the genus *Patellostium* Waagen) as in neither the holotype nor two paratypes is the exterior of the adult shell represented (Knight, 1941, p. 236, pl. 13, figs. 2a–c). Subsequently, he decided to institute a new generic name, *Patellilabia* Knight, for apparently the same gastropods, as he remarks that "Waagen, according to his diagnosis of

Patellostium, undoubtedly would have included in his genus the forms I include in *Patellilabia*" (Knight, 1945, p. 336). The advantage of having a complete and well preserved type for a genus is obvious, but the advisability of making a new name in place of old name for this sake may be questioned; by following this course we are liable to have new names perhaps for nearly half of our fossil genera, particularly the most familiar ones, what with so many types being not as well preserved as we now consider desirable, or being lost or destroyed. For this reason and for the sake of avoiding difficulty of references and confusion *Patellostium* is continued here as generic name as usual, while *Patellilabia* is accepted as subgeneric name for the species in which adult ornamentation is known.

PATELLOSTIUM (PATELLILABIA) MONTFORTIANUM (Norwood & Pratten) var. INTERMEDIA, n. var.

Pl. 1, figs. 1,2.

1855. *Bellerophon Montfortianum*. NORWOOD & PRATTEN, Acad. Nat. Sci. Phil., Jour., 2nd ser., v. 3, p. 74, pl. 9, fig. 5a–c.
1866. *Bellerophon Montfortianum*. GEINITZ, Carb. and Dyas in Nebraska, p. 8, pl. 1, fig. 13.
1866. *Bellerophon interlineatus*. *Ibid.*, p. 8, pl. 1, fig. 14.
1872. *Bellerophon Montfortianum*. MEEK, U. S. Geol. Survey Nebraska, Final Rept., p. 225, pl. 11, figs. 15,12(?)
1887. *Bellerophon Montfortianum*. HERRICK, Denison Univ. Sci. Lab. Bull., v. 2, p. 19, pl. 2, fig. 1; pl. 5, figs. 7–8A.
1915. *Patellostium montfortianum*. GIRTY, U. S. Geol. Survey Bull. no. 544, p. 172–174, pl. 20, figs. 1–3b.
1922. *Patellostium montfortianum*. MORNINGSTAR, Ohio Geol. Survey, 4th ser., Bull. 25, p. 251, pl. 14, figs. 13,14.

Several external molds, two of which are nearly complete, have a typical appearance of this common Pennsylvanian species of *Patellostium*. The well preserved greatly expanded (flaring) outer lip and revolving sculpture combined with transverse folds are characteristic of the genus and the species. The overall size of abt. 25 mm. is also typical of *P. montfortianum*, and also the insertion of finer revolving ribs between the regularly spaced coarser ones.

A closer comparison with the previously described and illustrated examples seems to disclose minor differences which may justify differentiation of the example from the Redoak Hollow as a variety of the typical form. Girty's illustrations of the example from the Wewoka of Oklahoma (1915, pl. 20, figs. 1–3b) are by far the most detailed among all previously illustrated examples, and a comparison with them shows the following differences in the example from the Wewoka: there are three finer ribs between each pair of coarser revolving ribs, and the transverse folds are prominent and sub-angular; in the example from the Redoak Hollow there seems to be only one finer rib between coarser revolving ribs, and its coarser ribs are not as coarse as those in the example from the Wewoka, and its transverse folds are rounded and only faintly indicated.

The examples from the Pottsville of the Flint Ridge of Ohio sketched by Herrick (1887, pl. 2, fig. 1, and pl. 5, figs. 7–8A) seem to be more nearly like the examples from the Wewoka than those from the Redoak Hollow, while the photographs of the material from the Mercer and McArthur limestones of the same area of Ohio are not sufficiently clear for close comparison of the sculpture.

Patellostium is rare in the Mississippian of America, and *P. branneri* Weller seems to be the only species known in the Mississippian of the South, in the Batesville sandstone of Arkansas. The single imperfectly preserved external mold illustrated by Weller (1897, pl. 21, fig. 9) and later by Girty (1915, pl. 11, fig. 6) has moderately developed transverse folds and only extremely faint revolving ribs. This is probably the ancestral form of *P. montfortianum*, as it is distinctly more like its example from the Redoak Hollow than that from the Wewoka. The form from the Redoak Hollow therefore could be provisionally designated as *P. montfortianum* var. (?) *intermedia*, n. var.

Genus BAYLEA de Koninck

BAYLEA [TREPOSPIRA] STELLAEFORMIS Hyde

Pl. 1, figs. 8,9

1953. *Mourlonia ? stellaeformis*, HYDE, Ohio Geol. Survey, Bull. 51, p. 325–326, pl. 46, figs. 1–4. Byer member, Logan formation, Waverly Series, Ohio.

Description.—The largest of the nearly complete external molds is about 3½ mm. in

diameter and slightly below 3½ mm. in height (probably with six volutions), but one fragment of the lateral part of shell indicates, by comparison with corresponding part of more nearly complete, but smaller shells, that the species grew up to 4 or 5 mm. across.

Faint, closely spaced revolving costae can be detected in the upper part of the upper slope, where it is flat to slightly concave, and similar revolving costae cover the lowermost part of the lower, inflated slope. Lines of growth are unusually strong for the genus. The slit-band is also unusually distinct (for the genus), being indicated by two strong revolving non-tuberculate costae, the upper costa being only slightly less prominent than the lower.

In the mature part of the shell (after it reaches 2 mm. or slightly over in diameter) the nodes that run just below the suture are transversely elongated, with intervals slightly wider than their width, about 14 nodes per one-half of a whorl. When diameter reaches nearly 3 mm. a second row of nodes appears just under the higher row, the nodes of the two rows lying close together along same transverse lines. The nodes of the lower row are slightly weaker than the nodes of the upper row, about 20–21 nodes per one half of a whorl at 3.5 mm. diameter. The pleural angle of the earlier 3 volutions is usually distinctly sharper than the angle of the mature volutions, so that the profile of the shell is concave (Pl. 1, fig. 9).

The species is common in localities 1 and 3. It is identical with the Waverlian form in all respects.

Discussion.—The Redoak Hollow species resembles the generotype *Trepospira sphaerulata* (Conrad) in its general inflated appearance, but is nearer to *T. depressa* (Cox), another Pennsylvanian species of the genus, in its sculpture. It differs from both of them in having very weak nodes just under the suture in the earliest 3–3½ whorls, changing to double rows of strong nodes in the mature whorls, and in being more prominently inflated below the slit band, a feature typical of genus *Baylea*.

In his comprehensive review of genus *Trepospira* Girty enumerates eight species, which "have been described from the Carboniferous of America, all of Pennsylvanian or at least post-Mississippian age" (Girty, 1915, p. 160–161), but he dismisses one of them, as only remotely related to *Trepospira* and reduces the others to only two valid species: *T. sphaerulata* (Conrad), the genotype, and *T. depressa* (Cox). Newell (1935) is inclined to recognize a larger number of species than Girty, but attempts no revision of all of them, and merely points out in which respects his new species *T. discoidalis* Newell (1935, p. 350–351, pl. 35, figs. 8a–11) differs from *T. kentuckiensis* and *T. illinoisensis*, which he considers valid species. He expresses belief that the forms described by Girty from the Wewoka of Oklahoma (1915, p. 158–161, pl. 21, figs. 6–11c), and also that illustrated by Plummer & Moore from the Mineral Wells and the Graham of Texas (1921, pl. 14, fig. 21; pl. 22, figs. 20–22) under the name *Trepospira depressa* Cox, "do not agree very well with Cox's species," which he believes was rightfully renamed *T. kentuckiensis* by Miller (1889). It is clear from Newell's discussion that he is recognizing the species of *Trepospira* on a combination of differences of such features as relative size, degree of sharpness of keel (lateral edge of shell), and tendency "for the upper surface of the whorls to be concave near the inner margin" as is the case in his species, as compared with the species from the Wewoka of Oklahoma. Girty, on the other hand, was inclined to regard such differences as "individual peculiarities" of a "not extremely variable species" (Girty, 1915, p. 162).

The new species from the Redoak Hollow has distinct transverse sculpture, while the later Pennsylvanian species have none, and besides, *T. stellaeformis* has lower part of whorls considerably more inflated than in all species of later age; and it is high spired in its early volutions, in contrast with much depressed early volutions and resulting flat top in all post-Redoak Hollow species. Finally, the new species has the slit band conspicuously marked by a pair of revolving costae, much more so than in *T. depressa* or other Pennsylvanian species. Girty made a shrewd observation when he said that, although the surface of the shell in the immature stages of his Wewoka form is not well shown, he has "some evidence for be-

lieving that during the earliest stage, that with rounded whorls, it was marked by transverse striae, extremely small in themselves but relatively coarse and strong for the size of the shell" (Girty, 1915, p. 160). The present evidence of prominent transverse sculpture in the adult whorls of the Redoak Hollow species, which is apparently ancestral to the species from the Wewoka, is fully compatible with the presence of similar sculpture in the embryonic volutions of the latter form. So is also compatible the inflated character of *T. stellaeformis* from the Redoak Hollow with the "rounded" character of the embryonic whorls observed by Girty.

All in all, the earliest representative of *Trepospira* helps much to determine its evolutionary trends, which are as follows: progressive increase of size, flattening of whorls, disappearance of transverse sculpture, and weakening of slit band.

The conspicuous inflation below the slit-band in the whorls of *T. stellaeformis* is unlike the rapidly receding lower slope typical for genus *Trepospira*, and it seems indicative of an affinity with the European Lower Carboniferous genus *Baylea* de Koninck (1883). Thanks to Knight's excellent photographs of *B. yvanii* (Léveillé), the generotype of *Baylea* (Knight, 1941, p. 51, pl. 21, figs. 1a–c), the sculpture of this form is so clearly illustrated that it can be compared in detail with that in *T. stellaeformis* (pl. 1, figs. 8,9). The comparison shows not only identical form of the whorls, but also considerable similarity in the sculpture, the only difference being the development of two rows of nodes in the upper slope just below the suture in adult *T. stellaeformis*. In *B. yvanii* this slope is sculptured only by the intersecting and nearly equally gentle revolving costae and lines of growth. This kind of sculpture can be recognized in the second whorl of *T. stellaeformis* (pl. 1, fig. 9, right side of second whorl from above), and it would be natural for it to be there if *B. yvanii* were its ancestor and the evolution from the latter toward the former proceeded in accord with the law of recapitulation. If this is the case, then it is permissible further to observe that the *Baylea* stage of sculpture has been "telescoped" into only one whorl, at the most, in *T. stellaeformis*, while in both *Baylea yvanii* and *Trepospira stellaeformis* the initial volutions are convex and sculptured by numerous thin revolving lirae, a situation suggestive of that in adult *Portlockiella* (Knight, 1945, p. 579–581), where *Turbopygmaeus* de Koninck from the Lower Carboniferous of Belgium is included. Hence an evolutionary lineage *Portlockiella —Baylea—Trepospira* can be at least tentatively suggested, *Trepospira stellaeformis* being an important link between *Baylea* and *Trepospira*. It can be thus designated as *Baylea* [*Trepospira*] *stellaeformis;* when being thus used as subgeneric name *Trepospira* is meant to indicate transitory stage toward more typical Pennsylvanian species of genus *Trepospira*.

Genus PHYMATOPLEURA Girty, 1939

1939. *Phymatopleura*, GIRTY, Jour. Wash. Acad. Sci., v. 29, p. 31.
1940. *Glabrocingulum*, THOMAS, Trans. Geol. Soc. Glasgow, v. 20, p. 35,38.

The name *Glabrocingulum* was introduced by Thomas (1940) for a Scottish Carboniferous gastropod which is generically undistinguishable from *Phymatopleura* Girty, and is its junior synonym.

PHYMATOPLEURA HETEROPLEURA, n. sp.
Pl. 1, figs. 10–12

The material is sufficiently distinct for its generic identification, and its well preserved sculpture presents an interesting combination of some features of the common gastropods described by Girty (1915) from the Wewoka of Oklahoma: *Phymatopleura grayvillense* (Norwood and Pratten). Indeed, Girty had some reasons to assign his two species to two different genera and introducing a new genus (*Orestes*, suppressed by Knight, 1941, p. 244, as synonym of *Phymatopleura*) for the reception of *P. nodosus*. The two species have considerable difference in the structure of the slit bands, and in the details of sculpture of the rest of the shell. However, the general configuration of their shells and fundamental design of sculpture are rather similar, and now the new material from the Redoak Hollow seems to supply the necessary additional evidence that indicates the common origin of *P. nodosus* and *P. grayvillense*, and allows to use for them both a single generic name *Phymatopleura*

Girty. On the other hand, though he expressed doubt of the correctness of the customary application of the name of the Devonian genus *Phanerotrema* Fisher for the Pennsylvanian gastropods, *P. grayvillense* and *P. marcouiana* (Girty, 1915, p. 149), he continued to classify them under this name, and later even added another species to this genus: *Phanerotrema brazeriana* (Girty, 1927, p. 430), but which is here referred to *Phymatopleura*.

P. heteropleura resembles *P. grayvillense* in the development of nodes along all of its six upper revolving costae, just as shown on the example of *P. grayvillense*, illustrated on Pl. 23, fig. 7 (Girty, 1915); also the costae which border the slit band are smooth in both of the compared species. On the other hand, *P. heteropleura* has its upper costae spaced quite different than in *P. grayvillense*, that has progressively wider spacing of these costae toward the top of whorls. In *P. heteropleura* the distances between second and third, and between third and fourth costae are about $1\frac{1}{2}$ as wide each as the average of the distances between each of the other pairs of six upper costae. In this respect its sculpture resembles that of the examples of *P. nodosa* illustrated on pl. 22, figs. 7 and 8c (Girty, 1915), though in these shells the upper revolving costae are somewhat more nearly equally spaced. It is the large width of the slit band, and the presence in it of a low central costa, sharp lines of inner demarkation of the border costae, and lunular design of the crossing lines of growth, that are very much alike in *P. heteropleura* and *P. nodosus*, particularly in the examples illustrated on pl. 22, figs. 8b (Girty, 1915). The comparison cannot be carried to the lower costae, as the lower part of the whorl is not preserved in the shell from the Redoak Hollow.

Although less than halves of two lower whorls are preserved, they are not flattened, and therefore their curvature and also their heights provide means for the judgment of the width of the shell, which must have been about $4\frac{1}{2}$ to 5 mm. The height of the lowest whorl is 2 mm., and that of the next above $1\frac{1}{4}$ mm. The poorly preserved remains of the two whorls above it, with their left side somewhat caved in, add another $\frac{3}{4}$ mm., which makes the total of $3\frac{3}{4}$ mm. height for the four whorls; probably one or two more whorls at the apex were present.

The sculpture of the next to last whorl, which is $1\frac{1}{4}$ mm. high and about $3\frac{1}{4}$ mm. wide, is the same as in the last whorl, and same or nearly same sculpture can be detected in the remains of the next whorl above, that must have been about $\frac{1}{2}$ mm. high. By comparison with the whorls of about same width and height in *P. brazerianum* var. *springerensis*, n.var., the sculpture of *P. heteropleura* is more prominent and angular, but the number and spacing of revolving and transverse costae are the same or nearly the same. One could define the sculpture of var. *springerensis* as

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EXPLANATION OF PLATE 1

FIGS. *1,2*—*Patellostium* (*Patellilabia*) *montfortianum* (Norwood and Pratten), var. *intermedia*, n. var. External molds; ×2.

3,4—*Euphemites compressus*, n. sp. Lateral and ventral views of holotype; ×10.

5–7—*Bucanopsis* (*Relispira?*) *reticulata*, n. sp. *5*, oblique view of external mold (holotype); ×10. *6*, fragmental external mold of another adult individual; ×10. *7*, lateral view of external mold of juvenile individual; ×10.

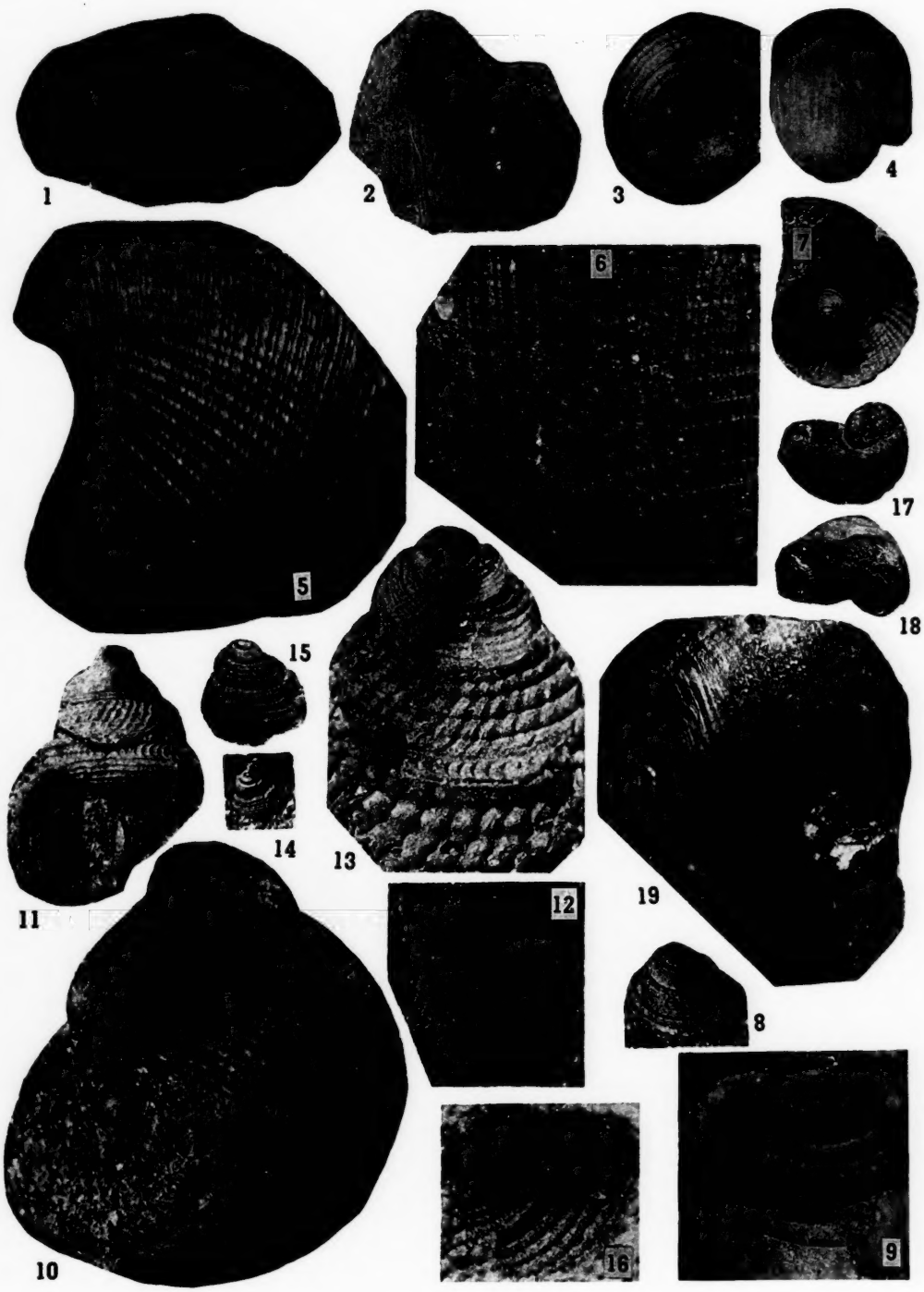
8,9—*Baylea* [*Trepospira*] *inflata*, n. sp. *8*, oblique view of external mold of a young individual; ×10. *9*, lateral view of external mold (holotype); ×10.

10–13—*Phymatopleura heteropleura*, n. sp. *10*, oblique view of external mold (paratype), ×10. *11*, lateral view of external mold of somewhat immature but complete individual (holotype); ×10. *12*, fragmental external mold of a large individual; ×10. *13*, lateral view of external mold (holotype), ×20.

14—*Phymatopleura brazerianum* var. *springerensis*, n. var. Lateral view of external mold of young individual; ×10.

15,16—*Amaurotoma* (?) *knighti*, n. sp. External molds. *15*, holotype; ×10. *16*, paratype; ×20.

17–19—*Strophostylus* n. sp. *17,18*, top and bottom views of internal mold; ×2. *19*, external sculpture of adult volution; ×10.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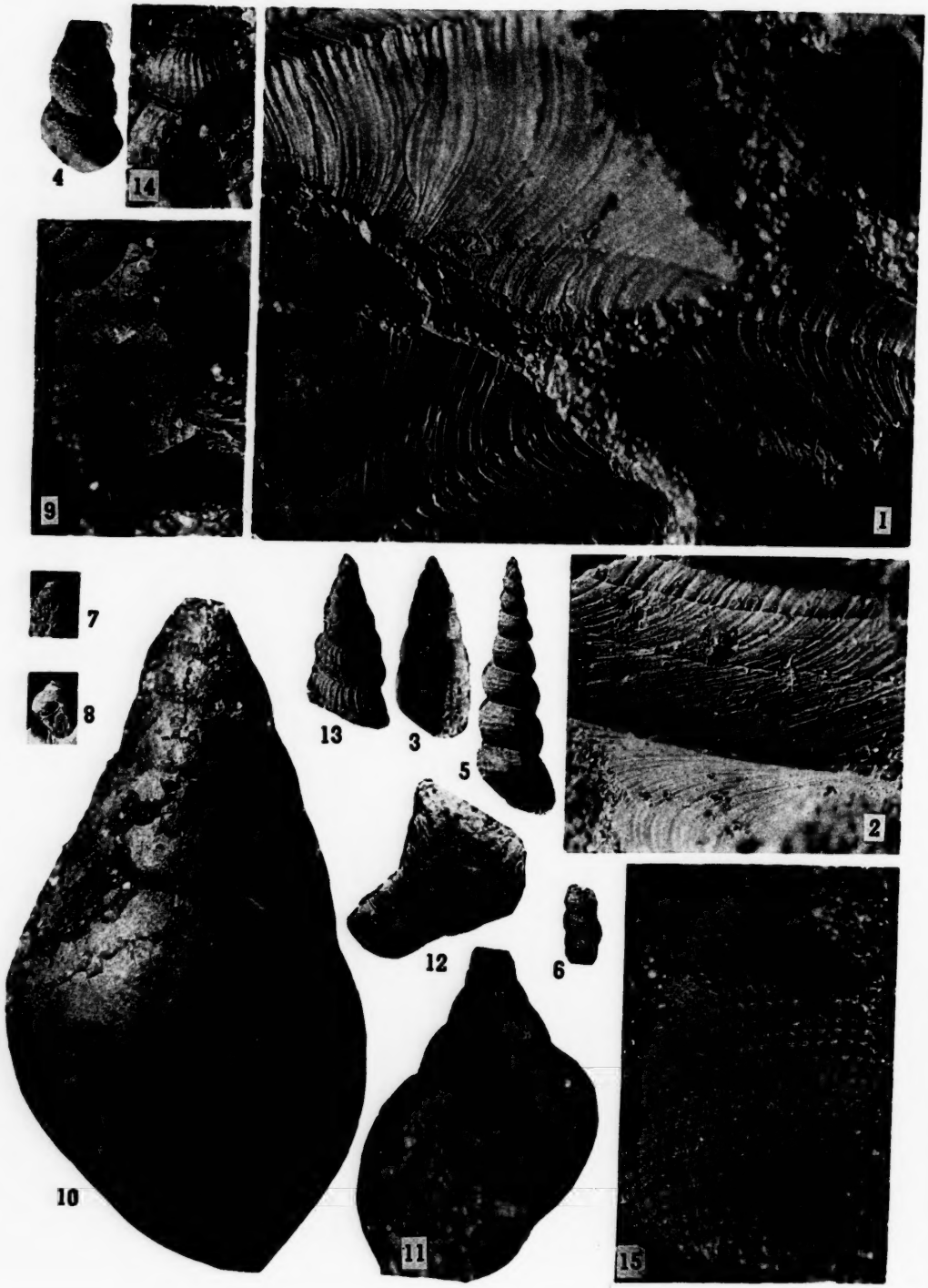
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a blurred version of that of *P. heteropleura*, the blurring affecting all prominence and depression, so that it appears that it could not be result of mere erosion. However, if it will be eventually proved that var. *springerensis* is merely the juvenile of *P. heteropleura*, the latter name should take precedence and be retained.

PHYMATOPLEURA BRAZERIANUM var. SPRINGERENSIS, n. var.
Pl. 2, fig. 7

The single shell (not mold) of this form, with an eroded apex, is so similar in all respects to *Phymatopleura brazerianum* (Girty, 1927, p. 430, pl. 25, fig. 25–27) that it can be identified with it assuredly. There is only one detail in the sculpture that permits to differentiate the form from the Redoak Hollow as a variety of the upper Mississippian *P. brazerianum*, and this is the presence of a low revolving costa in the middle of the silt band in var. *springerensis*. Girty does not describe or illustrate such additional costa, though he shows that the narrow slit band is crossed distinctly by numerous fine lunular transverse lines. In var. *springerensis* the slit band is also traversed by similarly spaced lines, but here they cross the medial costa, and each intersection results in a small knob, so that the median costa looks serrated.

In all other respects var. *springerensis* is like *P. brazerianum*. Its largest whorl is slightly over 2 mm. in diameter; its spire is moderately elevated; there are 6 or 7 revolving costae above and 12 below the slit; the upper costae are traversed by nearly equally strong transverse elevations, and in combination with revolving costae produce a cancellate sculpture. The lower 12 costae are subequal and not crossed by any transverse elevations. There is a distinct, but shallow umbilicus, a feature not mentioned for *P. brazerianum* by Girty perhaps because of poor preservation or concealment of it by the rock matrix.

Girty considered it necessary to compare critically *P. barzerianum* only with the obviously related common Pennsylvanian form "*Phanerotrema grayvillense*" (here treated as *Phymatopleura*), which is much larger than the Mississippian form, and hence, as he remarks, the observed differences in sculpture could be ascribed to their "very great difference in size." He puts greatest importance on "the absence of a swollen and nodose zone below the suture and the subdued character of the transverse markings on the under side of the final whorl, where the spiral lirae are not nodose as on the Pennsylvanian form" (Girty, 1927, p. 430). There is no tendency in var. *springerensis* to approach in these respects *P. grayvillense*, and thus it remains very close to the upper Mississippian species. Girty & Roundy (1923) list *Phanerotrema* n. sp., which is possibly *P. heteropleura* here described, among the forms identified from the Otterville limestone in the Ardmore Basin, but do not list there *P. grayvillense;* nor was it

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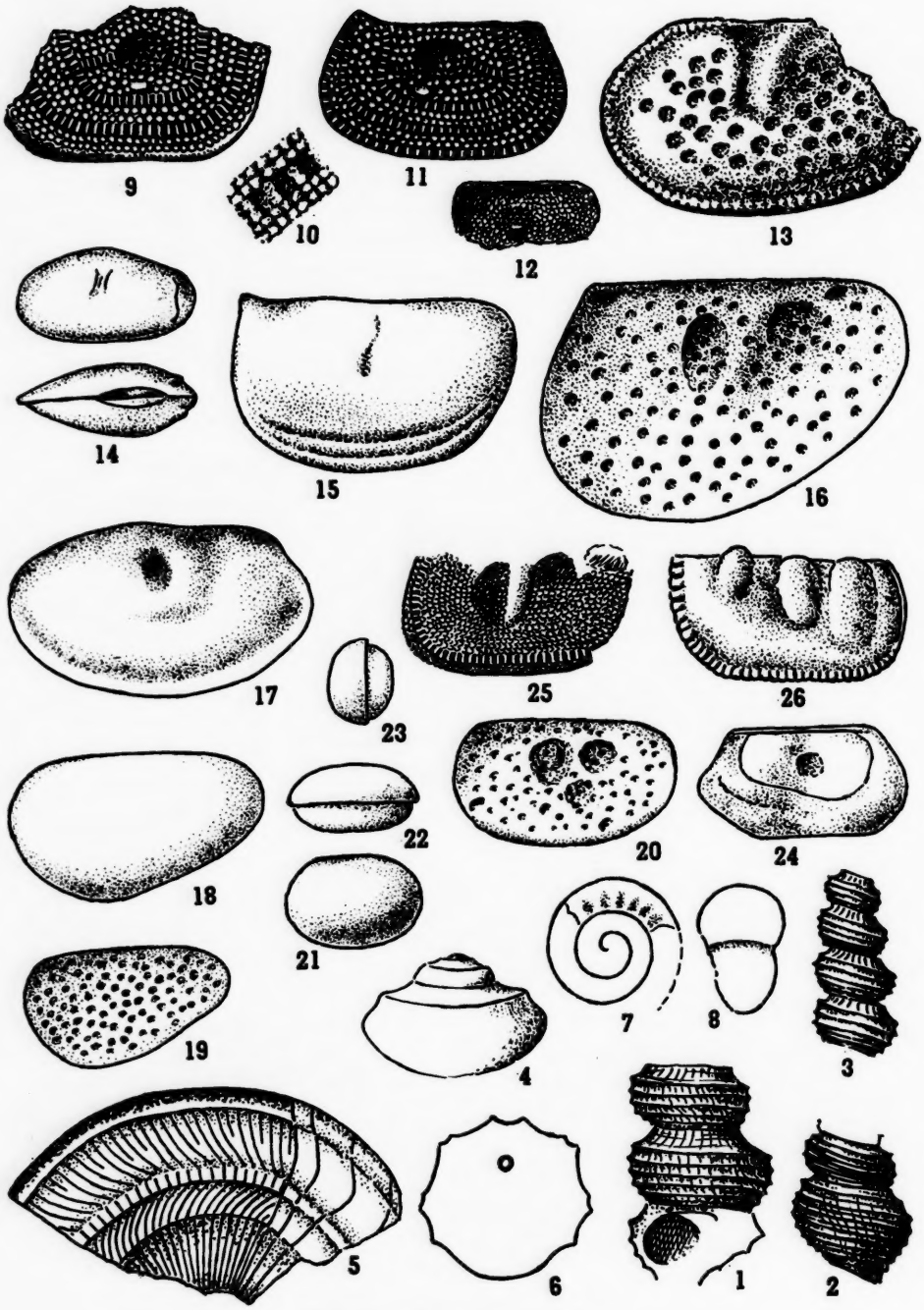
EXPLANATION OF PLATE 2

FIG. *1*—*Cerithiodes* (?) *gleanensis*, n. var. E. External mold of a fractured half-whorl. ×10.
2—*Murchisonia* (*Goniostropha*?) aff. *latei* Donald. External mold of a fragment of single whorl. ×10.
3—*Zygopleura* n. sp. *A*. Lateral view of external mold; ×10.
4—*Donaldina grantonensis* (Donald). Lateral view of external mold; ×10.
5—*Donaldina* cf. *tenuis* de Koninck. Lateral view of external mold; ×10.
6—*Donaldina attenuata* var. *ardmorensis*, n. var. Lateral view of external mold (holotype); ×10.
7—*Phymatopleura brazeriana* var. *springerensis*, n. var. Lateral view (holotype); ×2.
8–10—*Soleniscus* (*Macrochilina*) *regularis* (Cox), var. *8*, lateral view of incomplete juvenile individual reminiscent of *Sphaerodoma paludinaeformis*; ×2. *9*, lateral view of fragmental external mold of adult individual; ×10. *10*, lateral view of nearly perfect external mold of adult individual; ×10.
11—*Auriptygma primitia*, n. sp. Lateral view of external mold (holotype); ×10.
12—*Platyceras* (?) *acutirostris* Hall. Fragmentary external mold; ×2.
13,14—*Zygopleura* (*Cyclozyga*) *neotenica*, n. sp. Lateral view of external mold (holotype and paratype); ×10.
15—*Worthenia thomasi*, n. sp. External mold; ×10.



EXPLANATION OF TEXT-FIGS. 1–26

FIG. *1*—*Donaldina* cf. *tenuis* (de Koninck); ×15.
2—*Donaldina grantonensis* (Donald); ×15.
3—*Donaldina attenuata* var. *ardmorensis*, n. var.; ×15

found by Mather (1915) in the upper Morrow of Arkansas.

Genus AMAURotoma Knight

1858 (in part) *Pleurotomaria*, HALL, Albany Inst. Trans., v. 4, p. 21.
1859 (in part) *Pleurotomaria*, MEEK AND HAYDEN, Acad. Nat. Sci. Phila., Proc. 1858, p. 264.
1861 (in part) *Pleurotomaria*, MEEK AND WORTHEN, Acad. Nat. Sci., Phila., Proc. 1860, p. 252.
1882 (in part) *Cyclonema*, WHITFIELD, Am. Mus. Nat. Hist., Bull. v. 1, p. 75.
1906. *Cyclonema*, CUMINGS, 30th Ann. Rep. (1905), Dept. Geol. Nat. Res. Ind., p. 1344; Pl. 21, figs. 29–32.
1927 (in part) *Pleurotomaria*, GIRTY, U. S. Geol. Survey Prof. Paper 152, p. 427–428 and pl. 25, figs. 1–7 only.
1931 (in part) *Pleurotomaria*, SAYRE, Kans. Univ. Sci. Bull., v. 19, pt. 2, p. 132, pl. 14, figs. 3–36 only.
1933 (in part) *Yunnania*, KNIGHT, Jour. Paleontology, v. 7, p. 49; pl. 10, fig. 2a–f only.
1944 (in part) *Yunnania*, KNIGHT, *in* SHIMER & SHROCK, Index fossils of North America, p. 451, pl. 183, figs. 7,8 only.
1945. *Amaurotoma*. KNIGHT, Jour. Paleontology, p. 583–584; pl. 80, fig. 2a–e.

The genus *Amaurotoma* has been differentiated from *Pleurotomaria* (and subsequently from *Yunnania*) only after a very intensive and detailed work on American and foreign types, a tribute to the patience and persistence displayed by Dr. J. Brooks Knight. The old, very broad genus *Pleurotomaria* has now been split into a good dozen genera with about as beneficial an effect for taxonomic and stratigraphic paleontology as that which resulted from the splitting of such brachiopod genera as *Productus* or *Spirifer*. However, the work on revision of American pleurotomarid gastropod genera is still far from being completed, especially in regard to their Mississippian representatives. Knight considers the most distinctive characteristic of *Amaurotoma*, which separates it from very similar in shape and ornamentation *Yunnania*, the thinner columellar lip and a thinner shell. However, these characters cannot be recognized on specimens without apertures and represented by external molds only, as is the case with the small shells from the Redoak Hollow, which could be referred questionably to *Amaurotoma*. In this case the leading characters which seem to justify the classification with this genus are the roundness of whorls and their ornamentation with only revolving lirae, and the manner of spacing of the lirae and depressions between them, with a tendency to produce a plane to somewhat concave upper slope, upon which are developed revolving costae of second order crossed by nearly equally strong lines of growth. In the adult volutions of the genotype, *Pleurotomaria subsinuata* Meek and Worthen (1860), and in those of another species which Knight investigated in detail, *Pleurotomaria humerosa* Meek and Hayden (1859), the intersections of costae and lines of growth in the upper slope are produced into one or two rows of spines not far below the suture, but in the younger volutions the growth lines are much fainter

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4—Worthenia thomasi, n. sp. Inner mold; ×3.
5,6—Stroboceras furnishi, n. sp. Outer mold and cross-section; ×10.
7,8—(?) *Eumorphoceras girtyi* Elias. Young; lateral and dorsal views; ×10.
9–11—Amphissites bradfieldi, n. sp. *9*, outer mold of left valve; ×40. *10*, detail of ventral false keel, as viewed from its base, the keel being immersed in the matrix; ×100. *11*, outer mold of left valve of instar; ×60.
12—Roundiella bellatula Bradfield; outer mold; ×20.
13—Deloia sulcata Croneis & Funkhouser; ×40.
14—Healdia harltoni, n. sp. ×60, Upper figure, inner mold of left valve; lower figure, dorsum of inner mold.
15—Jonesina (?) sp. ×100 (undescribed).
16—Jonesina sp. cf. *J. spinigera* Cooper. Outer mold of left valve; ×80.
17—Carboprimitia sp. cf. *C. rotunda* Croneis & Funkhouser. Inner mold of right valve; ×40.
18—Paraparchites (?) sp. cf. *P. elongatus* Bradfield. Inner mold of right valve; ×40.
19—Paraparchites (?) sp.; ×40 (undescribed).
20—Hollinella sp. cf. *H. oklahomensis* Harlton. Outer mold of left valve; ×40 (undescribed).
21–23—Cavellina? sp. ×30 (undescribed).
24—Inner mold of valve of unknown ostracode (?); ×40 (undescribed).
25,26—Polytylites levinsoni, n. sp. Outer and inner molds; ×40.

than the revolving costae, and besides, there is a tendency toward division of the slope into two subequal halves by a rise of the lower of the two revolving costae located near suture. This tendency is more evident in *Pleurotomaria subsinuata*, and because the latter was selected as the genotype of *Amaurotoma*, it seems permissible to emphasize its general significance. This emphasis is eminently useful when considering Mississippian representatives of the genus. Knight himself classified in *Amaurotoma* the forms *Pleurotomaria levenworthana* Hall (1858) and *P. subangulata* Hall (1858) from the Salem limestone of Indiana, though he admits to "have seen no specimens of either species with growth-lines well enough developed or preserved to indicate the course of the outer lip" (Knight, 1945, p. 583–584). In neither of these two species are any spines produced on the upper slope, which is in harmony with the poor development of growth-lines, as observed by Knight. But instead the slope is divided by a single medial revolving costa. Hall describes it in his two species thus: in *P. levenworthana* "the first line below the suture uniformly thinner and sharper than the others, and the spaces on each side [from it] wider [than those between other revolving costae below]" (Hall, 1858, p. 94); in *P. subangulata* "midway between the [lateral] angle and the suture is one strong angular stria" (Hall, 1858, p. 24). In the Pennsylvanian representatives of *Amaurotoma* the mentioned sculpture of the slope, which seems so characteristic of the Mississippian species of the genus, too can be recognized, but only in earlier whorls, which fact is in good agreement with the law of evolutionary recapitulation, and points out naturalness of classification into one genus of these Mississippian and Pennsylvanian species. On the other hand it may be also pointed out that the upper slope in the two species from the Spergen of Indiana resembles that in *Pleurotomaria aspeniana* from the Brazer limestone of Idaho (Girty, 1927, p. 427–428, pl. 25, figs. 1–7), only in this form the division of upper slope is more pronounced through the development of angularity between the two halves of the slope, so that its upper half became sub-horizontal. So far Knight has not considered the gastropods from the Brazer in his revisions of Pleurotomarid group, but when he does so perhaps he will place *P. aspeniana* not in *Amaurotoma* but in another genus, or possibly erect for it a new genus. If so, a question may then arise whether *P. levenworthana* and *P. subangulata* should not be classified in the same genus with *P. aspeniana* rather than with *P. subsinuata*, an alternative also more suitable stratigraphically. No such reclassification is attempted here, however, as originals of none of the discussed forms are available for comparative study. Hence all of them are classified here with genus *Amaurotoma* in a broad sense, whose scope is expanded to embrace Girty's *P. aspeniana*.

AMAURotoma (?) KNIGHTI, n. sp.
Pl. 1, figs. 15,16

Two external molds of this small, low-spired form have been recovered. Both are made of four whorls, the lowest being about 1.6 mm. in diameter, with height of .8 mm., and the total height of conch 1.6 mm. Sutures are fairly deep, a feature distinguishing it from the contemporaneous genus *Rhabdocachlis* Knight (1933), whose conch is also very small. Whorls are ornamented by a number of sharp revolving costae separated by concave bands. Lower bands subequal, about half the width of each of the uppermost two bands, but the highest band, that is one below suture is slightly wider than the next band below, and is divided in the middle by a faint costa. The earliest volutions are more convex than the later ones, and the angle of spire is progressively wider toward the apex, where the spire is much depressed. In this respect the species is much like *Amaurotoma* (?) *aspeniana* (Girty), especially the smaller specimen of the latter illustrated by Girty (1947, pl. 25, figs. 1–3). On the other hand, in the roundness of whorls and the ornamentation of upper slope it stands closer to the two species from the Spergen, but these have a much higher spire. Hence *A. knighti* is specifically quite distinct from them all. It differs from the two known Pennsylvanian species (mentioned in the discussion of the genus) by the absence of rows of nodes in the upper slope.

A. knighti could be easily regarded as a young of *Phymatopleura heteropleura* (com-

pare figs. 13 and 15 in Plate 1) if it were not for the absence in its whorls of any transverse costae, which are clearly developed in all except the first volution of *P. heteropleura*.

Genus WORTHENIA Thomas
WORTHENIA THOMASI, n. sp.
Text-fig. 4; Pl. 2, fig. 15

Discussion.—Single fragment of adult or sub-adult whorl is referable to genus *Worthenia*, if the latter is to include species with differently proportionate upper and lower carinae than in all its previously described representatives. In all of them the upper carina projects out farther than the lower, that is "overhangs" it, and makes a strongly carinate shelf. In the new species it is the lower carina that projects out farther than the upper; besides, both carinae are less sharply "carinate." So subdued they are that the whole whorl is much like the rounded nepionic whorls of *Worthenia dunlopi* so well illustrated by Thomas (1940, pl. IV, figs. 3a,3b), especially its third whorl in which the lower carina projects farther away than the upper.

Description.—The only preserved whorl, if wholly restored, is apparently slightly more than 5½ mm. high, which is the distance from its preserved base to the beginning of only partly preserved, nearly flat concave upper face. Band (selenizone) narrow, only slightly prominent, situated on lower periphery of upper face and forming upper edge of a shallow sulcus less than 2 mm. wide. Its lower edge is marked by slightly wider and more concave groove between two revolving threads than grooves between threads above and below it. Lower edge is broadly rounded but projects much farther out than much sharper upper edge. Twenty revolving threads which cover gently rounded, 5½ mm.-wide lower face, are generally coarser than eleven threads that cover sulcus, and than three threads of upper face. Transverse "threads" paralleling lines of growth average strength of revolving "threads," and produce with them a characteristic reticulate pattern.

Comparison.—The species differs from all previously described representatives of *Worthenia* by its rounded instead of sharply angular whorls, and probably is less highly spired. In these respects it approaches the monotypic *Catantostoma* Sandberger of the Lower Devonian of Germany (Knight, 1941, p. 68–69; pl. 38, figs. 3a–d), the latter having still more rounded whorls. As already mentioned, *W. thomasi* is also much like the nepionic whorls of *W. dunlopi* Thomas from the Upper Limestone Group of Scotland (Thomas, 1940, table on p. 67), and which is now placed in zone E_2 or Arnsbergian of the Namurian by Currie (1954, table 1 on p. 532).

The reference of the Redoak Hollow fauna to zone E_1 makes it older than *W. dunlopi*, and this is harmonious with its similarity to the nepionic volutions of the latter. It also indicates the general evolutionary trend from rounded to angular conch, and thus allows to view the much rounded conch of *Catantostoma* as an ancestor to *W. thomasi*. This new species could well be considered new genus intermediate between *Catantostoma* and *Worthenopora*, but its erection is deferred pending more complete material.

CERITHIOIDES (?) GLEANENSIS, n. var. E.
Pl. 2, fig. 1

1926. *Cerithioides* (?) *gleanensis*, LONGSTAFF (*nee* DONALD), Quart. Jour. Geol. Soc. London, v. 82, pl. 35, fig. 4.

Fragments of this crushed gastropod are referred to European genus and species because of the well preserved sculpture, even if observed on fragments of two whorls. On the other hand neither the shape nor the sculpture of these fragments approach those of any known American Pennsylvanian or Mississippian gastropods.

The main fragment represents less than one half of circumferance of a single crushed whorl, and is fractured into two subequal portions; over it is centrally superimposed fragment of apparently a somewhat larger whorl. The face of the whorl is gently convex, with 1 mm. wide, centrally placed selenizone bordered above and below by sharp, but not very angular revolving costae. Lines of growth are fairly conspicuous, densely spaced, inequally strong, slightly accentuated when crossing the revolving costae. In the lower part of the upper slope of the volution a few very faint revolving costae can be recognized. The sinusoid design of the growth lines is sub-

stantially the same as can be observed in the sketch of *Cerithioides gleanensis* by Mrs. Longstaff (1926, pl. 35, fig. 4) except in her illustration the "crescents" of growth lines in selenizone are quite symmetrical about the middle of it, so that the upper and the lower ends of "crescents" are tangential to the border revolving costae. In our variety the would-be "crescents" of selenizone are much less curved and are asymmetrical, only their upper ends approaching tangential position to the revolving costa. In other words the outline of lines of growth curves backwards just as in *C. gleanensis* from Scotland but the selenizonal band in our form is superposed over the growth lines asymmetrically, so that the crest of the curve is being cut across by the lower bordering revolving costa. On the other hand all other details of sculpture correspond well: there is a slight costa-like angularity of the upper slope of whorl just below the suture, and below it the slope is for a short distance almost concave, and over the lines of growth are occasionally superposed very faint revolving lines, just as in the case of Scottish gastropod. However, our gastropod certainly attained a greater size than the single described individual from Scotland, whose length is 13 mm., width 6 mm., and width of selenizone is just a shade less than .5 mm. The probable over-all size of our form may be judged by the fact that its selenizone is 1 mm. wide, and total height (width) of whorl 5.5 mm., or about twice that of ultimate whorl in *C. gleanensis*.

It seems quite conceivable that the single described and illustrated example of *C. gleanensis* is not a mature shell of the species, but until this is proved to be the case it seems permissible to state that our form differs from it both in disposition of selenizone in relation to growth lines and also in larger size. It is designated as its new variety.

The Scottish species "is probably in the Upper Limestone Series" (Longstaff, 1926, p. 538). It has been compared with *Cerithioides* (?) *oweni* (Donald, 1895, p. 230–231, pl. 10, fig. 1) from the Yoredale (Namurian), and it seems also close to *Cerithioides telescopium* (Haughton) from the Lower Carboniferous of Cork and other localities in England (Donald, 1892, p. 573–574, pl. 17, figs. 1,4,5,8). The form from the Yoredale is as small as *C.* (?) *gleanensis*, while that from the Lower Carboniferous is about two times larger than our Redoak Hollow form. Both of these English species differ from *C.* (?) *gleanensis* and *C.* (?) *gleanensis* var. *E* in having selenizone perfectly smooth, but otherwise are quite comparable with them in shape and sculpture.

It may be also mentioned that two species of *Pleurotomaria* (*Foordella*) described by Longstaff (1912, p. 300–303, pl. 29) from the Lower Carboniferous of Ireland, have sculpture of whorls very similar to that of our form from the Redoak Hollow, but the whorls in subgenus *Foordella* are proportionally much more convex, on account of which Mrs. Longstaff referred these species to the genus *Pleurotomaria* instead of one of the subgenera of *Murchisonia*.

No representatives of *Cerithioides*, which was one time considered a mere section or subgenus of *Murchisonia*, have been previously recorded in America.

MURCHISONIA (GONIOSTROPHA?) sp., aff. M. (G?). TATEI Donald
Pl. 2, fig. 2

1892. *Murchisonia* (*Goniostropha*) *tatei*, DONALD, Quart. Jour. Geol. Soc. London, v. 48, p. 563–564, pl. 16, fig. 2.

The single fragment of a whorl from the Redoak Hollow is probably a new species and possibly even a new section (or subgenus) of *Murchisonia*. But since it would be entirely impractical to erect new systematic unit on such small fragment, it is here compared with the British Lower Carboniferous shell that seems nearest to it in many respects, while no known American Mississippian or Pennsylvanian gastropods can be so compared.

The outstanding feature of the fragment is its proportionally very wide selenizone, and its location at a sharp angle directly below a sharp revolving costa that terminates the gently concave upper slope of a whorl. This upper whorl resembles in its details the nature of the slopes and sculpture of two species of *Murchisonia* in the lower Carboniferous of England, which Donald (1892, pl. 16, figs. 2,3–7) classifies in sections (subgenera) *Goniostropha* and *Hypergonia*. The characteristic features of this upper slope is its gentle concavity, and two

distinct though faint revolving costae located somewhat closer to the suture above than to the selenizone below. However, the fragmentary whorl from the Redoak Hollow has its lines of growth at a sharper angle, particularly where they cross the costa of the selenizone, and this selenizone is oriented at a sharper angle to the upper slope, and is wider than any known among the discussed British forms, though it is nearest to those in *M.* (*Goniostropha*) *tatei.*

Genus ZYGOPLEURA Koken

1892. *Zygopleura.* KOKEN, Neues Jahrbuch f. Mineralogie, v. 2, p. 25.
1930. *Pseudozygopleura.* KNIGHT, Jour. Paleontology, v. 4, Supp. 1, p. 13.
1933. *Zygopleura.* LONGSTAFF (*nee* DONALD), Quart. Jour. Geol. Soc. London, v. 89, p. 90.
1941. *Pseudozygopleura.* KNIGHT, Geol. Soc. America Spec. Paper no. 32, p. 282.

American gastropods which are here referred to *Zygopleura* have been classified originally by Meek and Worthen with the Silurian genus *Loxonema* Phillips, the latter genus being expanded to include all related later species up to and including those from Triassic. Subsequently Koken introduced the genus *Zygopleura* for geologically later representatives of the comprehensive *Loxonema,* including there the forms ranging from Devonian to Triassic. In 1930 Knight attempted phylogenetic classification of loxonemid gastropods, and concluded that Koken's *Zygopleura,* based on a Triassic generotype, did not evolve from the Carboniferous–Permian group of loxonemid genera, but evolved from Devonian *Loxonema* as a side line through an unknown post-Devonian pre-Triassic lineage. This conclusion led him to the introduction of the genus *Pseudozygopleura* for the shells from the Lower Carboniferous–Lower Pennsylvanian previously classified as *Zygopleura.* He pointed out that the shells of *Pseudozygopleura* differ from true *Zygopleura* in having the transverse ribs in the early 3 or 4 volutions with very strong angularity, instead of being more nearly vertically straight, as is the case with *Zygopleura.* The early volutions of the Triassic species of this genus, examined by Knight on European (St. Cassian) material of which Knight examined at the Peabody Museum of Yale University, are described as "composed of five smooth, unornamented volutions, followed immediately by whorls having strong, typical zygopleuroid costae" (Knight, 1930, p. 7).

However, according to the subsequent investigation by Longstaff of the same (St. Cassian) loxonemid gastropods in the British Museum (Natural History) disclosed the fact that in many Triassic species, when their early whorls are well-preserved, they are ornamented by "fine curved ribs similar in character to, though not so strong as, those on the latter part of the shell." Furthermore, she finds this is "also the case with the British Carboniferous forms, and where the early whorls are smooth this condition is evidently from wear, since better preserved examples of the same species have the ornamentation intact." (Longstaff, 1933, p. 91). Hence Longstaff finds no difference between *Zygopleura* and *Pseudozygopleura,* and uses the former name for the Carboniferous forms of England.

It seems that until further comparative investigation of Triassic and late Paleozoic loxonemid gastropods Longstaff's understanding of the genus *Zygopleura* should be followed, in which case *Pseudozygopleura* becomes its junior synonym.

ZYGOPLEURA sp. *A*
Pl. 2, fig. 3

Description.—Only a single example of this species has been recovered, and external mold of incomplete spire, its apex missing.

The preserved part of the external mold consists of four and a half whorls making a high spire with pleural angle approximating 15°. Individual whorls are about twice as wide as high, ornamented with transverse, nearly straight vertical ribs, over which are superposed very faint equidistantly spaced revolving costae. The ribs have an angular profile, with the slope of the angular rib which faces aperture being somewhat longer than the opposite slope. Shorter slope is occasionally marked by one faint stria, and longer slope by one or two such striae.

Discussion.—Formal name is not given to the new form because of its incomplete preservation. It is related to *Zygopleura wortheni* (Weller) (1916, p. 261, Pl. 18, figs. 18–20) from the St. Genevieve limestone of

Illinois; *Zygopleura kellettae* (Knight) (1930, p. 49–50, Pl. 2, figs. 15a,b) from the Labette shale of the upper Des Moines Series at St. Louis, Missouri; and *Zygopleura robroystonensis* var. *tenuicostata* Longstaff (1933, p. 102, Pl. 8, fig. 3, Pl. 12, figs. 8,9) from the Upper and Lower Limestone series of the Carboniferous in Scotland.

Sculpture of neither Scottish nor American forms mentioned has been described in as much detail as just given for the form from the Redoak Hollow, but the faint revolving costae can be seen at some places on the photographs reproduced by Weller, Knight and Longstaff. These forms are so closely related that they could be referred to the same species if it were not for the difference in the number of transverse costae per volutions of same size. In the volutions which are .5 mm. high there are about 8 transverse ribs in *Z. kellettae*, while there are 10 ribs in .5 mm. high volution in *Z. wortheni* and *Z. tenuicostata*. In the volution of same size in the example from the Redoak Hollow the number of ribs is also 10, but it differs from them in having higher spire (15°) than in *Z. wortheni* (32°) and *Z. tenuicostata* (25–30°). *Zygopleura roskobiensis* Longstaff (1933, p. 100, pl. i, fig. 15) is about as high spired as the form from the Redoak Hollow but differs in larger number of costae.

Subgenus Cyclozyga Knight

1930. *Cyclozyga*, Knight, Jour. Paleontology, v. 4, Supp. 1, p. 19,20,74–75, pl. 5, figs. 7,8,15.
1936. *Cyclozyga*, Knight, Jour. Paleontology, v. 10, p. 520.
1941. *Cyclozyga*, Knight, Geol. Soc. America Spec. Paper no. 32, p. 91–92, pl. 49, fig. 1.

When Knight introduced the genus *Cyclozyga* he considered it "as the climax of the *Plocezyga—Hemizyga—Hyphantozyga* line of orthogenetic changes in that it is completely without transverse ornamentation, or at most the transverse lines are very weak in comparison with the few, strong revolving ribs or keels." *Hyphantozyga*, a subgenus of *Hemizyga*, which is distinguished by sub-equal development of revolving and transverse ornamentation, is considered a side-line and not in direct ancestry to *Cyclozyga* (Knight, 1930, p. 20 and diagrams of evolution on p. 10 and p. 20). Knight (1936, p. 520) subsequently designated *Cyclozyga mirabilis* as holotype of the genus, apparently because in this species the transverse sculpture disappears completely in adult volutions. In the second known species, *C. carinata*, fine transverse costae remain in the adult volutions, although the revolving carinae which are located in the lower ⅔ of the volutions, greatly predominate over the transverse costae.

Zygopleura (Cyclozyga) neotenica, n. sp.

Pl. 2, figs. 13,14

Description.—Two external molds of a moderately high-spired representative of Pseudozygopleurinae are suggestive of *Cyclozyga*, and yet an outright classification with this genus may be questioned because of the peculiar behavior of the revolving keels which are superimposed, as it were, over its prominent transverse costae. Revolving keels appear for the first time in the third whorl, gain prominence in the next three whorls, and nearly fade out in the last two or three whorls. In view of the opinion by Knight, quoted in the discussion of the genus *Cyclozyga*, that the development of the revolving keels in the "Pseudozygopleurinae" is an evolutionary advance, it seems that the present example indicates the development of such keels in the adolescent stage, from which apparently this evolutionary innovation spread over the adult stages in a later geological time; hence the specific name *neotenica*. Following is the description of this form. Conch moderately high-spired, with moderately shallow sutures; consisting of eight whorls, which total 2.5 mm. high with about 1.2 mm. diameter of the last whorl, basal part of which is broken off. The first whorl is quite smooth and subspherical; the second bears only transverse costae, which are comparatively fairly coarse; the third bears the same kind of costae plus one sharp revolving keel just above the suture, and a very faint second keel a little higher; the fourth and fifth volutions have three sharp keels each, one just above the suture, and two other spaced at equal intervals above, so that the third or highest keel occupies position a little below the middle of volution (counting the space from suture to suture); in the sixth and seventh volutions the first or basal

keel is fairly sharp, but the second keel is very faint and the third fades out completely; judging by the absence of revolving keels in the preserved upper two-thirds of the eighth whorl it has the same kind of ornamentation. The transverse costae continue to remain equally strong over all the lower volutions, with a general slight progressive increase in strength with increase in size of each succeeding whorl. In the last whorl there are 8 transverse costae per 1 mm.

Discussion.—In the species from the Red-oak Hollow the ornamentation consists of equally prominent revolving and transverse costae; yet they are not combined in the same manner as the equally prominent revolving and transverse ornamentation developed in the subgenus *Hyphanthozyga* Knight (1930, p. 18–19, 73–74, pl. 5, figs. 5,6). In the latter they produce reticulate pattern, which is not like that in *Z. neotenica;* only in the lower part of the volutions in the latter species the sculpture may be considered reticulate, but the effect of the whole sculpture is rather that of heterogeny, an unmixed occurrence in the same whorls of zygopleurid type of sculpture (with transverse costae only) and cyclozygid type (with revolving costae only). It seems that it is this kind of shell, where the revolving costae apparently just begin to develop, as they appear in the lower part of the adult volutions only, and do not extend, at this stage, over their upper part, where transverse lirae as yet preserve their whole strength—may be considered in or very close to the direct ancestry to the more typically developed series of *Cyclozyga: C. carinata* and *C. mirabilis.* Also, because the sculpture of the lower half of the volution in *Z. neotenica* is reticulate, it could be in direct ancestry to subgenus *Hyphantozyga.* The stratigraphic position of *Z. neotenica* at the end of Mississippian time is in harmony with such interpretation. Among a number of British species of *Zygopleura, Z. scalaroidea* (Phillips) from the zones D_2–D_3 of the Visean in England seems to stand close to its ancestral Lower Carboniferous stock (see Longstaff, 1933, p. 97–98, pl. 9, figs. 11–13). It has the same type of laterally flattened whorls ornamented with "vertical thin ribs not continued on the base, where these are merely fine threads" (ibid., p. 97), and the number of ribs in a whorl is almost the same. In some of Longstaff's photographs a few revolving costae can be clearly discerned at the base of mature whorls (*ibid.*, pl. 9, figs. 12,13), a situation which could have developed into that of *Z. neotenica.*

Thus, an evolutionary development of this species from an ancestral comprehensive genus *Zygopleura* seems obvious, the regular coarse costae, being stabilized over the whole conch (except the initial volution or protoconch?), which is moderately high spired, being quite typical for the genus. The development of the few revolving keels, as described, is a step toward the genus *Cyclozyga,* which at this stage of evolution perhaps could be considered rather a subgenus of *Zygopleura.* The situation is similar to the above discussed case of the evolutionary development of *Derbyia* from *Orthotetes,* and therefore the same taxonomic treatment of the genus *Cyclozyga* as a subgenus of *Zygopleura* is followed here for the evolutionary stage of its inception.

Genus DONALDINA Knight

1881. *Aclisina* DE KONINCK, L. G., partim, Ann. Mus. Roy. d'Hist. Nat. Belgique, sér. paléont., v. 6, p. 86.
1889. *Aclisina* MILLER, S. A., North American Geology and Paleontology, p. 395.
1898. *Aclisoides* DONALD, Quart. Jour. Geol. Soc. London, v. 54, p. 48.
1919. *Aclisina* MARK, C. G., in Condit, Ohio Geol. Survey, (4) Bull. 17, p. 314, pl. 16, figs. 7–10.
1931. *Aclisina,* KNIGHT, J. B., Jour. Paleontology, v. 5, p. 1–11, pl. 1.
1933. *Donaldina,* KNIGHT, J. B., Jour. Paleontology, v. 7, p. 57–58.
1941. *Donaldina,* KNIGHT, J. B., Geol. Soc. America Spec. Paper 32, p. 104–105, pl. 48, fig. 3a–c (includes no reference to change of generic name to *Donaldina* for the American Pennsylvanian species previously described under name *Aclisina*).

Generotype.—Aclisina grantonensis Donald, 1898, p. 60; Lower Carboniferous of Scotland.

Some confusion has been introduced in application of name *Aclisina* to Pennsylvanian species in America because Donald (1898), overlooking the fact that Miller (1889) designated *A. striatula* as generotype for de Koninck's genus, selected for the same purpose *A. pulchra,* and named the same *A.*

striatula as genotype of her new genus *Aclisoides*. Knight, too, at first (1931) overlooked Miller's designation of the genotype, but later (1933) corrected the error, and introduced the new generic name *Donaldina* for the group where *A. pulchra* belongs, but selected for genotype of this new genus *A. grantonensis* Donald instead of *A. pulchra* (de Koninck) because the latter is "insufficiently known to serve with complete satisfaction as a genotype" (Knight, 1933, p. 57). Knight further specifically stated that "the three American Pennsylvanian species discussed in the previous paper of this series (Jour. Pal., vol. 5, 1931) thus become *Donaldina robusta* (Stevens), *D. stevensana* (Meek and Worthen), and *D. swalloviana* (Geinitz)," and so will be referred to *Donaldina* also all other American forms previously classified as *Aclisina*. Hence in its new sense, and since Knight's introduction of the name *Donaldina*, there are no true representatives of *Aclisina* (=*Aclisoides*) s.s. found in America. No reference to this taxonomic situation has been incorporated in the Geol. Soc. America Spec. Paper 32, which became the standard reference book on the Paleozoic gastropod genera of the World, and no cross-reference is given there to Knight's own decision in this matter.

All high-spired gastropods from the Redoak Hollow which are ornamented with revolving lirae thus are referrable to *Donaldina* and neither to *Aclisina* s.s. nor to *Murchisonia*. Since they are the oldest known representatives of *Donaldina* in America their relationship to British Lower Carboniferous species of the genus is of particular interest, and it will be shown that some of them are apparently identical with the latter forms.

DONALDINA ATTENUATA var. ARDMORENSIS, n. var.

Text-fig. 3; Pl. 2, fig. 6

1898. *Aclisina attenuata*, DONALD, Quart. Jour. Geol. Soc. London, v. 54, p. 58–59, pl. 4, figs. 2,3.

1917. *Aclisina attenuata*, DONALD, Quart. Jour. Geol. Soc. London, v. 73, p. 70.

?1917. *Aclisina micula*, DONALD, Quart. Jour. Geol. Soc. London, v. 73, p. 71, pl. 5, fig. 7a,b.

Among the known American forms the new variety resembles most the common Pennsylvanian form *Donaldina stevensana* Meek and Worthen. The most complete study of the latter was done by Knight (1931, p. 8,9, pl. 1, figs. 1a–g, text-figs. 1,a,h), who collected a very large number of its individuals from the Labette shale, Marmaton group, Des Moines series, from the outcrops in the vicinities of St. Louis, Missouri; but the variety is still closer to the British Lower Carboniferous form *D. attenuata*, as will be shown below.

The four individuals from the Redoak Hollow, and particularly the most complete among them, selected as holotype, have smaller length than the shells of *D. stevensana* that have the same number of whorls, and this in spite of the fact that the earliest volutions in *D. attenuata* var. *ardmorensis* not only are not compressed vertically, but that they are not shorter than wide, as is the case with the juvenile whorls in *D. stevensana*, but, on the contrary, have even a larger height in proportion to width, than the adult volutions of both the new variety and *D. stevensana*. The adult whorls in the latter are almost twice as wide as high, and the juvenile whorls in *D. stevensana* are two to three times as wide as high, while in *D.* var. *ardmorensis* the whorls tend to become as high as wide in the early part of the shell. In other characters of the shell the two species display many characters in common. They are equally high spired and have the same or nearly the same sculpture. The sculpture in *D.* var. *ardmorensis* consists of one wide, slightly concave band at the top of each whorl, and below it are five narrower concave bands divided by very narrow costae. The highest of these fine bands is the widest among them, and the bands below it gradually diminish in width just as illustrated for *D. attenuata* by Donald (1898, pl. 4, fig. 2). On the other hand the narrow lower bands in *D. stevensana* are subequal. Furthermore, Knight's observation of "somewhat cuesta-like" profile of the "lirae" (five elevations are called so by Knight, 1931, p. 25) with the steep face toward the spire" (Knight, 1931, p. 8) does not seem to apply to the costae in *D.* var. *ardmorensis*, which appear rather symmetrical, with equal slopes on either upper or lower sides. The variety differs from *D. attenuata* by its slightly larger side and by the presence of lines of growth in the uppermost band (just under suture).

DONALDINA GRANTONENSIS (Donald)
Text-fig. 2; Pl. 2, fig. 4

1878. *Murchisonia striatula*, R. ETHERIDGE, JR., Quart. Jour. Geol. Soc. London, v. 34, p. 19, pl. 2, fig. 29.
1898. *Aclisina grantonensis*, DONALD, Quart. Jour. Geol. Soc. London, v. 44, p. 60, pl. 4, figs. 7–9.
1933. *Donaldina grantonensis*, KNIGHT, Jour. Paleontology, v. 7, p. 57.
1941. *Donaldina grantonensis*, KNIGHT, Geol. Soc. America Spec. Paper 32, p. 104–105, pl. 48, fig. 3a–c.

Donaldina grantonensis was designated as generotype by Knight and in connection with this move he investigated it in some detail and reproduced photographs of two paratypes (1941, pl. 48, figs. 3b,3c), a desirable addition to previous illustration in form of sketches only. Four specimens from the Redoak Hollow are placed in this species: a mature part consisting of 2½ whorls, including the ultimate one (fig. 2), and the other two representing middle, immature part of shell. They agree with the examples from Scotland in practically all instances: size, shape, and sculpture, and if there are departures in details of sculpture, which do not exactly match those illustrated or described on Scottish examples by Donald and by Knight, they seem to be well within the variability of this species.

Most characteristic for the species is small size, comparatively large (for the genus) pleural angle (13°), well developed lines of growth, and—particularly—intercalation of median costae of second order between some of the fairly numerous coarse revolving costae of first order. It is in the detail of disposition of these costae that variability within the species can be noted when descriptions and illustrations by Donald and by Knight are compared. Thus, as Donald (1898, p. 60) describes: "the lower two thirds of each whorl ornamented by about nine raised threads, alternately coarse and fine; upper third apparently smooth." Knight's (1941, p. 105) description, based on paratypes in Bennie's collection at Royal Scottish Museum, Edinburgh (holotype has not been available for his study) reads as follows:

"The lirae divisible into two groups of different character, upper and lower, the upper lirae occupying about one-third the whorl face, being very fine and faint, the lower lirae, about eight in number, occupying the lower two-thirds of the whorl face and being coarser, with occasional finer lirae intercalated between them."

From a comparison of the descriptions (where terms "raised threads," "lirae," and "costae" mean the same revolving elevations upon the face of whorls in gastropods), one can note that whereas Donald lists nine alternately coarser and finer costae in the lower two thirds of the whorls, Knight lists eight with "occasional" finer ones between them, which implies total number larger than nine. Because Knight's photograph of mature example (pl. 48, fig. 3c) has been taken under light whose direction tended to emphasize lines of growth rather than revolving costae it is somewhat difficult to compare the disposition of the latter in his and Donald's illustrations, costa for costa. It appears likely, however, that both descriptions are based on actual observations, though on different examples; this is indirectly supported by the fact that the corresponding sculpture observed on the examples from the Redoak Hollow is in a way intermediate between what these two authors observed. Thus, the sculpture of our mature example is as follows: the upper one-third of whorl is ornamented by very fine regularly spaced four or five costae, while the lower two-thirds are covered with equidistantly spaced seven coarse costae. The upper five of these delimit four gently convex bands, with only occasionally discernible very faint trace of costae of second order between them, while the lower costae delimit two equally wide bands, but in each of these is developed a quite distinct costa of second order. By comparison with the observations and illustrations by Donald and Knight, the example from the Redoak Hollow seems to indicate greater regularity of the development of second order costae than as implied by Knight, but on the other hand all its well developed second order costae occur in the lower part of the lower two-thirds of the whorls, whereas Donald claims their overall development in an "alternate" order. However, in her first described and therefore presumably most typical example (1898, pl. 4, fig. 7), and which was designated by Knight as holotype (Knight, 1941, pl. 48, fig. 3a, republished by Donald), the finer costae of second order are shown prominently only in the lower two bands, but in

the upper three or four bands above them only very faint costae are indicated (Donald, 1898, pl. 4, figs. 7,7a). The total length of first example is 1.6 mm. and maximum diameter .7 mm.

The mature example from the Redoak Hollow (fig. 2) consists of two and a half whorls. It is similar to *D. grantonensis* in size, shape, and general character of sculpture, that consists of both revolving costae of two orders, and growth lines. The upper one-third of whorl is marked by four or five regularly spaced, very faint costae; while the lower two-thirds are ornamented by six equidistantly spaced coarse costae between which are intercalated second order costae. The latter costae are much weaker than the costae of first order in the upper three gently concave bands, but in the lower three bands they are just about as strong as the costae of first order, so that the lower part of whorl appears to be ornamented by coarse costae of the first order only, but spaced twice as densely as the first order costae just above. Hence in this example the prominence of all second-order costae is proportionally greater than that in the first example so that higher second order costae are quite distinct, and the lower second order costae are nearly as prominent as those of first order. The total length of this example is 1.6 mm., and maximum diameter .75 mm.

One of the remaining two fragmentary examples consists of three whorls from mature part, with over-all length of 1.6 mm., and with .75 mm. maximum diameter. The whorls are ornamented in the lower two-thirds by five coarse equidistantly spaced costae; three upper concave bands between these costae are concave and smooth, the fourth has very faint costa of second order, and the lowermost has a more distinct second order costae. The upper one-third of the whorl is covered by three or four very faint costae.

The fourth example is also an immature 2½ mm. long part of shell. It consists of five whorls with maximum .85 mm. diameter. Each whorl is ornamented by five coarse costae, with a faint costa of secondary order in the lowermost band only. Hence in all examples from the Redoak Hollow here referred to *Donaldina grantonensis*, the upper three to four bands in the lower two-thirds of volution have no costae of secondary order or they are very faint.

All Scottish examples of the species were collected from the Calciferous Sandstone series of the Lower Carboniferous.

DONALDINA sp. cf. D. TENUIS (de Koninck)
Text-fig. 1; pl. 2, fig. 5

1881. *Aclisina pulchra*, L. G. DE KONINCK, Ann. Mus. Roy. Hist. Nat. Belg., v. 6, pt. 3, p. 87, pl. 7, figs. 26,27.
1883. *Murchisonia tenuis*, L. G. DE KONINCK, *ibid.*, pt. 4, p. 22, pl. 32, figs. 3,4.
1898. *Aclisina pulchra* var. *tenuis*, DONALD, Quart. Jour. Geol. Soc. London, v. 54, p. 52–54, pl. 3, figs. 1–5.
1916. *Solenospira pygmaea*, WELLER, Contr. Walker Mus., Univ. Chicago, v. 1, p. 256, pl. 18, figs. 1–6.

Description.—External mold of nearly complete spire with mature whorls ornamented by six to seven revolving costae, marking five to six depressed bands. The upper two bands are subequal, while the lower ones diminish in width gradually downwards. The subequal lines of growth can be observed all throughout the shell when light is thrown across them. The upper slope occupies slightly more than ⅓ of the width of volution, and in it can be observed three very faint costa. One is near its base, and two others near its top, the latter two being developed only in the ultimate volution.

Discussion.—The Redoak Hollow form resembles *D. tenuis* closely in general shape, pleural angle, and details of ornamentation. However, it is only less than half the size of the original Belgian shells described by de Koninck, and it would be hazardous to identify it with the latter if it were not for the fact that Miss Donald expanded the concept of the species *tenuis* to include Scottish examples which include smaller varieties, some as small as the discussed specimen from the Redoak Hollow. It is interesting to observe, however, that the sculpture of our specimen is more nearly like that in the larger Scottish form (Donald, 1898, Pl. 3, figs. 2,4) than that in the forms whose size is about the same as in ours (ibid., pl. 3, fig. 5). It seems quite possible that this merely shows considerable variability of the shell in this European species, and that illustrated representatives of it cover only a small fraction of the existing variations. On the other

hand, perhaps the comprehensive species will be eventually split into subspecies and varieties with a more restricted stratigraphic range for each: it ranges through the Lower Carboniferous of Europe. The form from the Ste. Genevieve described by Weller (1916) as *Solenospira pygmaea* is similar to *D. tenuis* in broad sense and displays about same range of variability.

PLATYCERAS (?) sp. cf. P. ACUTIROSTRIS Hall
Pl. 2, fig. 12

The single fragment representing the greater part of one side of a *Capulus*-type shell can be only doubtfully compared with *Platyceras acutirostris* of the upper Missisippian on the evidence of undulating lines of growth. Indeed somewhat similarly undulating are also the lines of growth in Pennsylvanian species *P. spinigerum*, but in this and two other similar Mississippian species the sculpture of the shells is spinose, which is obviously not the case in the fragment from the Redoak Hollow. The tentative comparison with *P. acutirostris* is certainly not tantamount to identification, which is difficult for the fossil Capulidae even when complete and undistorted shells are available. Even its generic classification with *Platyceras* is uncertain.

SOLENISCUS (MACROCHILINA) REGULARIS (Cox), var.
Pl. 2, figs. 8–10

1857. *Loxonema regularis*. COX, Ky. Geol. Survey, v. 3, p. 566, pl. 8, fig. 2.
1858. *Macrocheilis fusiformis*. HALL, Iowa Geol. Survey, Rept. v. 1, pl. 2, p. 718, pl. 29, fig. 7.
1866. *Polyphemopsis chrysalis*. MEEK & WORTHEN, Ill. Geol. Survey, v. 5, p. 596, pl. 28, fig. 7.
1881. *Soleniscus* (*Macrocheilis*) *fusiformis?*. WHITE, U. S. Geol. Survey. W. 100 Merid., Supp. App. p. xxix, pl. 4, fig. 4a–c.
1894. *Bulimorpha inornata*. KEYES, Mo. Geol. Survey, v. 5, p. 265, pl. 55, fig. 6.
?1915. *Bulimorpha minuta*. GIRTY, Mo. Bur. Geology and Mines, 2nd ser., v. 13, p. 362, pl. 29, figs. 4–4b (Cherokee ser.)
?1915. *Sphaerodoma paludinaeformis*. GIRTY, U. S. Geol. Survey, Bull. 544, p. 207, pl. 24, figs. 5,6,6a.
1931. *Soleniscus* (*Macrochilina*) *regularis*. KNIGHT, Jour. Paleontology v. 5, p. 220–223, pl. 24, fig. 2a,b, pl. 27, fig. 10.

This list is only a part of the synonymy of the species published by Knight (1931, p. 220–221) in connection with his comprehensive study of Subulitidae, perhaps the most difficult family of Paleozoic gastropods. As Knight further testifies "this species as represented not only in the synonymy but in my own collections has been a particularly difficult to deal with," and adds that if there are "more than one species in my collections and in the synonymy . . . I am at a loss to distinguish them." Taking in to account the attention given to this and other gastropods by the mentioned author it would be presumptious for me to try to improve on his synonymy, except by putting two forms described by Girty in 1915 under question mark, thus reflecting rather Knight's own doubt about these forms, as expressed in the text of his contribution. These observations have some bearing on the identification of the well preserved outer mold from the Redoak Hollow, which is identical in all respects with some of the junveile, $\frac{1}{3}$ to $\frac{1}{2}$ grown specimens illustrated by Knight, if the latter were magnified two or three times. These are particularly Knight's specimens pl. 24, figs. 2d and 2e, which are most inflated, with sides distinctly convex, among all illustrated by him. The comparison between these and other specimens suggests evolutionary tendency within the stock toward greater slenderness and larger size, the full grown examples of *S. regularis* illustrated by Knight (1931, pl. 24, figs. m,n, and o) having straight instead of convex sides. Correspondingly, their pleural angle is sharper that that in the earliest stages of growth (1931, pl. 24, figs. d and e). Only one good specimen of this form has been secured from the Redoak Hollow, and in view of this the conclusion just stated is tentative, and the form is considered mere variation of *Soleniscus regularis*.

AURIPTYGMA sp. *A*
Pl. 2, fig 11

Only one external mold of this form has been recovered, but its completeness and fine preservation of ornamentation allow detailed comparison with the previously described species of the genus. Only American species are of interest in this respect, as they come from the lower Pennsylvanian (Marmaton group of the Des Moines series) the foreign (original) species being from the

Silurian of Bohemia. The Redoak Hollow form is small for the genus and very robust, particularly for its size. It consists of six or possibly seven volutions, the rapidly growing inflation resulting in distinct concavity of the sides. In these respects the new species resembles closely *A. simplex* Knight (1931, pl. 25, figs. 3a–f); it is also much smaller than the latter, or the other two species described by Knight. The Redoak Hollow form has distinct, even though faint, growth-lines, resembling those seen in *A. simplex* (Knight, 1931, pl. 25, fig. 3a). Our outer mold is not sufficiently preserved for observation of columella and details of the aperture, but the latter seems typical of *Auriptygma* in its general configuration. Following are the dimensions of *A.* sp. *A:*

Height, circa 5.4 mm.; width, 3.6 mm.

Knight has made a bold move when placing the Silurian *Auriptygma fortiar* (Barrande) Perner in the position of being the ancestral stock for American Pennsylvanian species, with no intermediate form being known anywhere in the Devonian and lower Carboniferous. The present discovery of *Auriptygma* sp. A in the Redoak Hollow fills partially the gap, and supports the phylogeny proposed.

Strophostylus sp. *A*
Pl. 1, figs. 17–19

One nearly complete shell and an internal mold of another have been recovered. They consist of about three not very tightly coiled and very rapidly expanding volutions, very low spire, closed umbilicus and only growth lines ornamenting the shell.

A thorough revision of genus *Strophostylus* Hall (1860, p. 22, pl. 118, figs. 2) was undertaken by Knight (1941, p. 341–342; pl. 87, figs. 1a,b), who also revised the related Carboniferous genus *Anomphalus* Meek & Worthen (Knight, 1941, p. 37–38, pl. 6b, figs. 3a,b. Thanks to this revision and publication of ten times enlarged figures of the tiny holotype, its distinction from *Strophostylus* is so well established that generic assignment of the new species from the Redoak Hollow to *Strophostylus* can be assuredly made. It is not as tightly coiled as *Anomphalus*, and because of that the sutures between the coils are distinct, while *Anomphalus* has no sutures. Besides, *Strophostylus* is much larger than *Anomphalus*.

Strophostylus sp. *A* is not unlike the two previously described Mississippian species: *S. carleyanus* Hall and *S. splendens* Girty from the Moorefield and the Batesville of Arkansas (Girty, 1911, p. 94, pl. 8, fig. 6; and 1915, p. 124–125, pl. 11, figs. 11–13a), but it differs from both by much larger size, sinuous curving of the lines of growth, and by the presence of a few very faint revolving costae in the lower part of the last volution. It is 20 mm. long, while the above mentioned species described by Girty are 5 and 6½ mm. long respectively. Easton (1942, pl. 10, fig. 18) published an apertural view of "*Strophostylus* sp." from the Pitkin of Arkansas, judging by which the form was about 25 mm. long, but absence of description or of other views of this shell makes its complete comparison with *Strophostylus* sp. *A*, impossible.

The common Pennsylvanian species *S. nana* Meek and Worthen is even smaller (4 mm. × 5 mm.) than the Mississippian forms described by Girty and has non-sinuous growth lines. It has been recorded by Beede & Rogers (1908, tables of the stratigraphic distribution of the invertebrates p. 371,383) ranging from the upper part of the Des Moines to the top of the Pennsylvanian.

Discussion of the Gastropods

Perhaps the chief characteristic of the whole group of gastropods from the Redoak Hollow is their overwhelming affinity to the Lower Carboniferous forms (see Table 1); they are about equally divided between those from the American Mississippian, and those from the Lower Carboniferous of England. The combination of these two affinities outweighs their affinity to the Lower Pennsylvanian forms in a ratio of about three to one.

The strongest among the Pennsylvanian affinities is that displayed by *Petalostium*, a genus as yet unknown below the basal Pennsylvanian anywhere in the World; and also by two smooth, inflated, medium-spired species of *Soleniscus-Auriptygma* group, most species of which were until recently classified under *Sphaerodoma* with a very broad understanding of this genus (Girty, 1915, p. 191–216). But even these two latter forms seem to be also not very distantly related to *Anematina proutana* (Hall) and *Naticopsis carleyana* (Hall) from the Spergen of In-

TABLE 1.—LIST OF THE GASTROPODS FROM THE REDOAK HOLLOW WITH AN INDICATED RELATIONSHIP TO THE KNOWN EARLIER AND LATER FORMS

Mississippian	Redoak Hollow Formation	Lower Pennsylvanian
Euphemites urii Weir	*Euphemites compressus*, n. sp.	*Euphemites carbonarius* Cox
Bucanopsis textilis (Hall)	*Bucanopsis (Retispira?) reticulata*, n. sp.	*Bucanopsis meekiana* Swallow
	Patellostium (Patellilabia) cf. *montfortianum* (Norwood and Pratten), var. *intermedia*, n. var.	*Patellostium montfortianum* (Norwood and Pratten)
Baylea [Trepospira] stellaeformis (Hyde)	*Baylea [Trepospira] stellaeformis* (Hyde)	*Trepospira depressa* (Cox)
Phymatopleura braazerianum Girty	*Phymatopleura brazerianum* var. *springerensis*, n. var.	*Phymatopleura nodosa* (Girty)
Phymatopleura brazerianum Girty	*Phymatopleura heteropleura*, n. sp.	*Phanerotrema grayvillense*
	Amaurotoma (?) knighti, n. sp.	
Amaurotoma (?) aspeniana Girty	*Amaurotoma (?) aspeniana*, n. var. D	
	Worthenia thomasi, n. sp.	
Cerithioides gleanensis Longstaff	*Cerithioides (?) gleanensis*, n. var. E	
Murchisonia (Goniostropha) latei Donald	*Murchisonia (Goniostropha?)* aff. *latei* Donald	
Turbonopsis	*Turbonopsis* (?), sp. F	
Zygopleura tenuicostata Longstaff	*Zygopleura*, sp. A	*Zygopleura kellettae* (Knight)
Zygopleura scalaroides Phillips	*Zygopleura (Cyclozyga) neotenica*, n. sp.	*Hyphantozyga gracilis* (Knight)
Donaldina attenuata (Donald)	*Donaldina attenuata* var. *ardmorensis*, n. var.	
Donaldina grantonensis (Donald)	*Donaldina grantonensis* (Donald)	
Donaldina tenuis (de Koninck)	*Donaldina* cf. *tenuis* (de Koninck)	
Platyceras acutirostris Hall	*Platyceras* cf. *acutirostris* Hall	
Anematina proutana Hal	*Solensicus (Machrochilina) regularis* (Cox)	*Soleniscus (Macrochilina) regularis* (Cox)
Elasmonema	*Auriptygma*, sp. A	*Auriptygma simplex*
Strophostylus splendens	*Strophostylus*, sp. A	*Strophostylus nana*

Note: Solid lines indicate identity or close relationship of the species; dotted lines indicate their more distant relationships.

diana, the different generic assignment of the two Mississippian forms being more apparent than real. Thus, it seems conceivable that when the smooth-shelled, medium-spired gastropods are eventually collected in a satisfactory state of preservation in beds of Chester age they may be found to be of intermediate character between Aleramecian genera *Anemiatina* and *Soleniscus* (*Macrochilina*) on one hand, and Pennsylvanian genera *Naticopsis* and *Auriptygma* on the other.

Other plani-coiled gastropods besides the already mentioned *Petalostium*, though not much different from the trivial lower Pennsylvanian forms, *Euphemites carbonarius* and *Bucanopsis meekiana*, can be about as easily compared with the pre-Namurian forms from England, *Euphemites urii*, and even more so with American late Mississippian forms, such as *Bucanopsis textilis* (from the Spergen).

Another group of gastropods whose affinities with Mississippian and Pennsylvanian forms are about equally strong or only with a slight edge in favor of Pennsylvanian, are here classified in the genus *Amaurotoma*, other species of which were previously known under the generic names *Cyclonema* (Ordovician genus) or *Pleurotomaria* (Jurassic genus), both classifications are now being abandoned; also is abandoned their classification with the genus *Yunnania* (from the Upper Carboniferous of Indo-China), where Knight placed them prior to 1945. As mentioned already much more conspicuous are the affinities of the Redoak Hollow gastropods with some Lower Carboniferous European forms. Here belong particularly several groups of high-spired, conspicuously ornamented gastropods popularly known as *Murchisonia*, *Zyglopleura* and *Aclisina* (now renamed *Donaldina* by Knight). Altogether there are 8 species which appear to be migrants from the region of the British Isles and adjacent part of Europe, and they make up to 40% of the gastropods from the Redoak Hollow. Even if it is true that a few species of *Murchisonia*, *Zygopleura* (usually identified as *Loxonema* and *Pseudozygopleura*) and *Aclisina sensu lato* have been occasionally identified among the gastropods of the American late Mississippian, the latter do no look much like the forms from the Redoak Hollow and certainly less than their British Isles generic equivalents, and this fact constitutes the most peculiar character of the discussed fauna. A similar situation in regard to some Redoak Hollow pelecypods has been already pointed out, and the similar conclusion about British affinities of the just mentioned gastropods places emphasis on apparent mass migration of mollusks from British—West European seas to the south-central part of North America at the end of Chester time (the inaugration of Redoak Hollow time).

Abundance of the high-spired, well orna-

mented gastropods of the same *Murchisonia—Zygopleura—Aclisina* affinities in the upper part of the Des Moines, as revealed by their monographic treatment by Knight, indicate their probable persistent abundance in population of the early Pennsylvanian seas of the Mid-Continent, even if their presence is seldom recorded. Very few of their representatives are barely mentioned by Mather in the Morrow of Arkansas, and *Zygopleura* and *Aclisina* are mentioned in the lists of identifiable fossils from the Dornick Hills formation of the Ardmore Basin by Girty & Roundy (see Tomlinson, 1929, p. 73–75). It seems likely that further collecting of these small gastropods will furnish some links between the species from the Upper Des Moines described by Knight. Perhaps when this job is completed the whole fauna of the Redoak Hollow gastropods will appear more nearly balanced in its Mississippian and Pennsylvanian affinities, but this anticipated emendation of the situation cannot possibly change the fact now revealed, that these groups of high-spired gastropods are descendants of migrants from the Lower Carboniferous of western European seas rather than derivatives of the American Mississippian forms. It is interesting to note finally, that the group of pleurotomarid gastropods in the Redoak Hollow fauna is represented by *Phymatopleura* and *Amaurotoma* with strong affinity to the Chester (Brazer) forms from Idaho.

AMERICAN MOLLUSKS IN THE BASAL MILLSTONE GRIT FAUNA OF SCOTLAND

The present intensive comparative study of many groups of Carboniferous invertebrates resulted in experience in re-evaluating the evolution of various Carboniferous stocks and gentes, which can be now applied to the re-evaluation of previously published works on stratigraphically similar or related transtitional invertebrate faunas. Till now only one important fauna (Table 2), comparable to the Redoak Hollow, was discovered in the British Isles from the localities east and southeast of Glasgow (Hind, 1908). This fauna is fairly well preserved, stratigraphically distinct, and comprises numerous forms. It is a combination of several collections from the marine bands occurring less than 100 feet above the base of the Millstone Grit. Each of these was found "not far below the line which has been drawn between the Upper and Lower Carboniferous floras, in accordance with Dr. Kidston's determinations" (Hind, 1908, p. 322). Tait writes to Hind that "from the upper part of the Millstone Grit at Castlecary, plants belonging to the Upper Flora were obtained, so that the horizon at which the flora changes is almost the same level as that in Midlothian" (Hind, 1908, p. 333–334), which is the coal-field area and south, where the stratigraphy and position of fossils were harmoniously worked out at several outcrops. The combined marine faunas from several localities are thus placed at the very top of the Lower Carboniferous, if defined by the change in terrestrial plants, or at the base of the Upper Carboniferous, if defined by the lithology of the Millstone Grit. The total fauna consists of two corals and nine brachiopods, none of which were described or illustrated; thirty-two pelecypods, seven gastropods and one scaphopod, all of which

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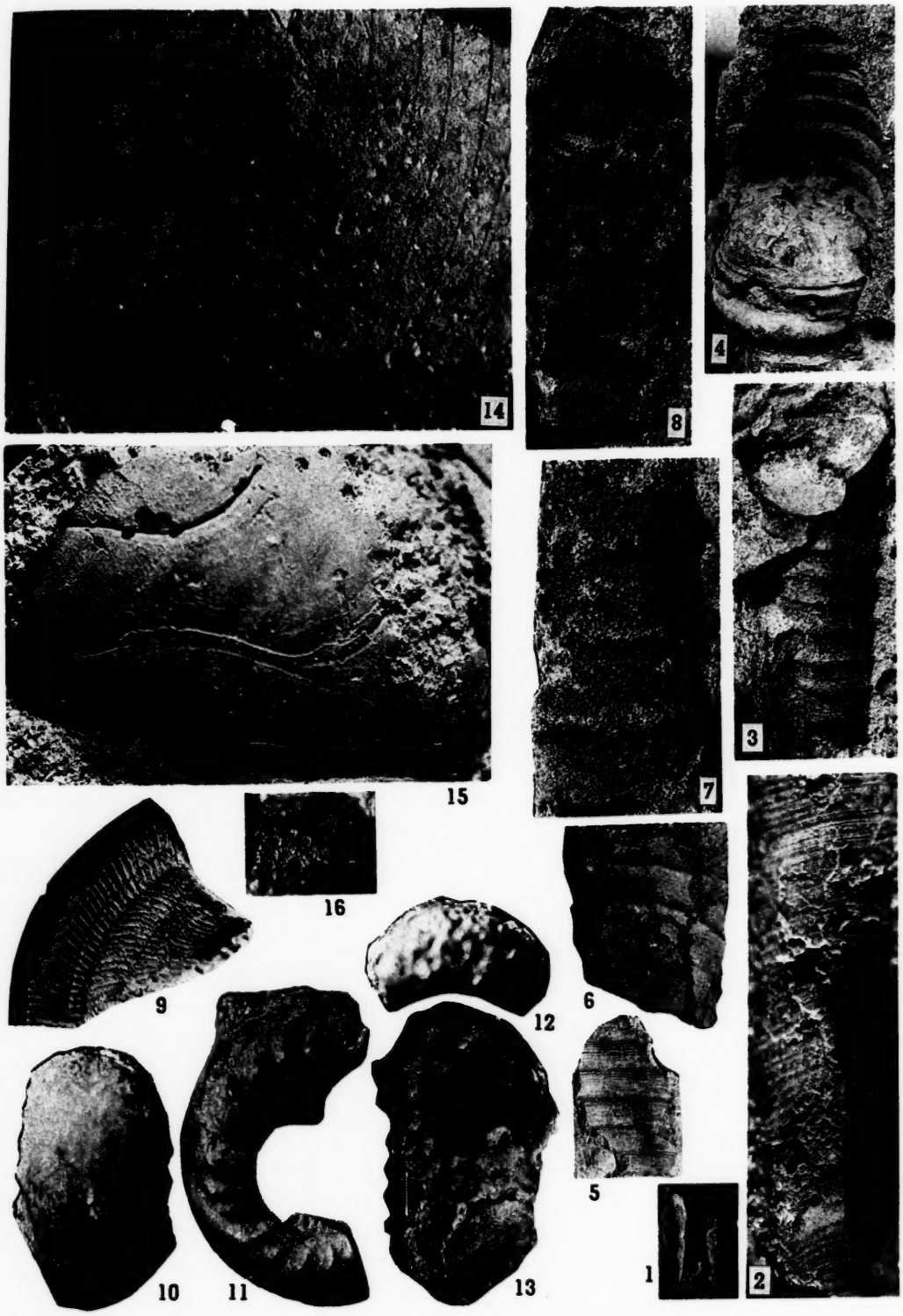
EXPLANATION OF PLATE 3

FIG. *1—Laevidentalium* sp. cf. *L. venustum* (Meek & Worthen). Internal and external molds; ×2.
2—Plagyoglypta annulostriatum (Meek & Worthen). External mold; ×10.
3–6—Cycloceras meeki, n. sp. ×2. *3,4*, external mold (holotype). *5*, internal mold (paratype). *6*, external mold (paratype).
7,8—Cycloceras randolphensis Worthen. Internal and external molds; ×2.
9—Stroboceras furnishi, n. sp. Outer mold; ×10.
10–13—Eumorphoceras girtyi Elias. ×10. *10,11*, dorsal and side view of same specimen. *12,13*, front and dorsal view of another specimen.
14,15—Cravenoceras sp. *14*, external mold of ventral part of adult volution, with numerous molds of outer circular depressions of *Cyclopuncta girtyi*, n. gen., n. sp. (holotype); ×10. *15*, internal mold of lateral part of an adult volution; ×10.
16—External mold of problematic shell with molds of circular depressions of *Cyclopuncta girtyi*, n. gen., n. sp.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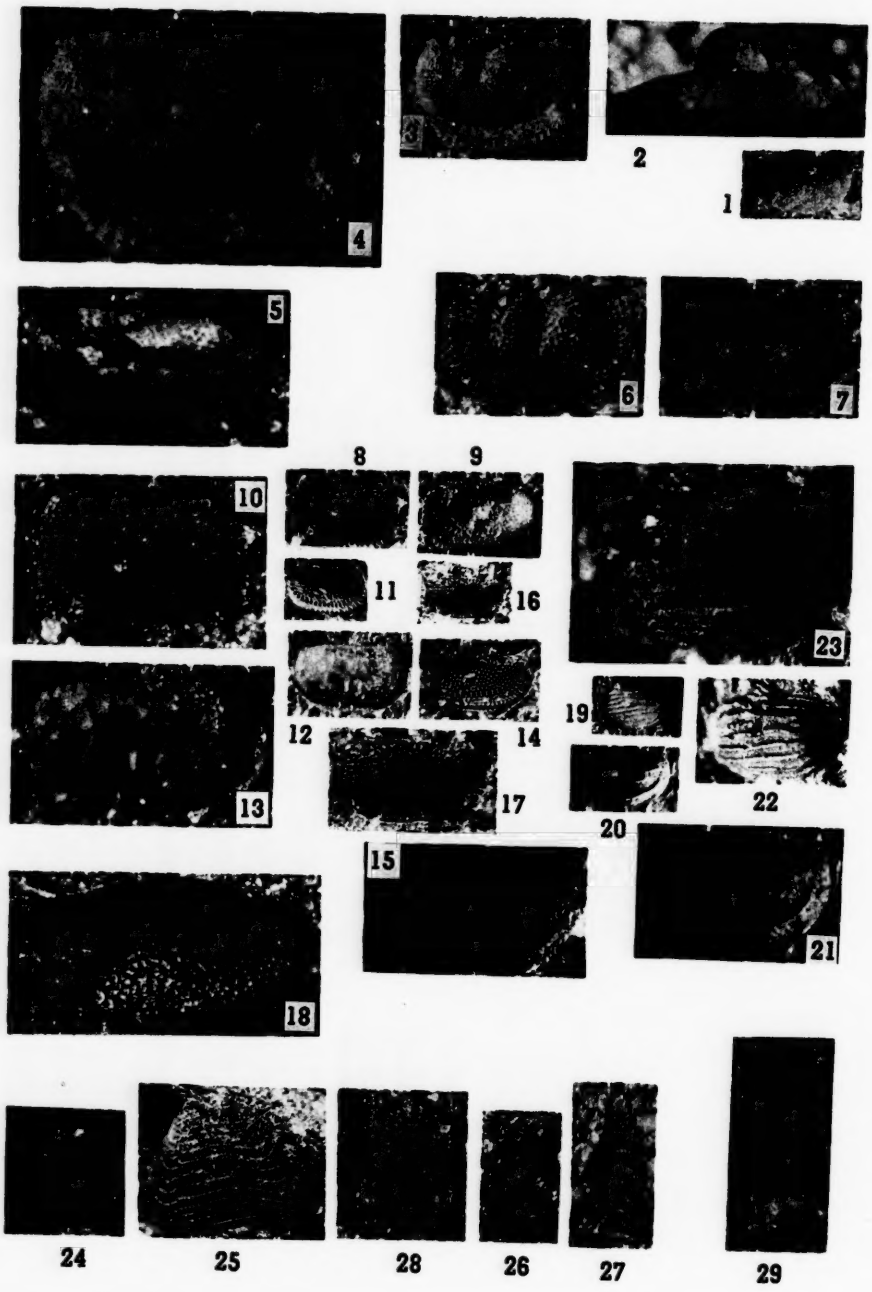
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were described and illustrated by Hind (1908). The pelecypods comprise the bulk of all these faunas, and it is a species of an undoubted typical American pelecypod, *Prothyris*, that started Hind's conclusion that among the lamellibranchs of the collections "quite 50 per cent of the species were, as far as I could discover, new to Europe, but which resemble very closely the lamellibranch fauna of the Coal Measures of Nebraska and Illinois of North America" (Hind, 1908, p. 332). Elsewhere (p. 333) he asserts that the gastropods of the collection "show a strong relation to the North American fauna." He makes no such claim, however, for the corals or brachiopods, as he finds them related to forms from the underlying Upper Limestone series of the Lower Carboniferous, a situation reminiscent of the invertebrates in the Redoak Hollow in relation to the earlier Late Mississippian forms of America.

In general, Hind's discovery of the relationship of mollusks in the basal Millstone Grit of Scotland to American forms may still be considered correct (see the list of reidentification of his forms in Table 2), but, in many instances, his identifications were undoubtedly erroneous, because of limited information on American early Carboniferous mollusks available to him at that time. Correction of his identifications of bellerophontid (planicoiled) gastropods was made by Weir (1931), and now other gastropods and many pelecypods are being reidentified on the evidence of Hind's illustrations and descriptions. The latter task would be hazardous if it were not that Hind's illustrations are known for their accuracy, Weir's testimony about this being particularly important. Although his monograph on Carboniferous Bellerophontidae is illustrated by superb photographs, he did not attempt to reillustrate Hind's *Bellerophon* because he finds that "Hind's figure is good, and shows well the determinable features of the shell" (Weir, 1931, p. 812). In both Weir's and the present reidentifications some gastropods and pelecypods claimed by Hind to have American affinities are shown to be related to the known European rather than American forms. American affinities of others are difficult to deny, and new evidence is added here which was impossible to point out at Hind's time. Only after his 1908 paper was published, did a series of papers by Girty describing upper Mississippian invertebrates of Arkansas and Oklahoma appear, and this made possible their adequate comparison with European Carboniferous forms. Stewart Weller's 1897 pioneer work on the Batesville fauna apparently escaped Hind's attention. It was far less complete, especially in regard to mollusks, and was not as well illustrated as the subsequent revision and description of late Mississippian faunas by Girty. Hence, Hind was in a position to compare his Millstone Grit forms with some degree of assurance only with the Upper Carboniferous forms of Nebraska and Illinois, as worked out by Geinitz, Meek, and Worthen. If his claim of affinity of some of

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EXPLANATION OF PLATE 4

FIGS. *1–4—Hollinella radiata*, var. *dotti*, n. var. *1*, inner mold of instar, which has no flange; ×20. *2*, profile of internal mold of adult valve showing conspicuous elevation of anterior (left) and posterior nodes; ×40. *3,4*, external mold (holotype); × 20 and ×40.

5—Kirkbya symmetrica Croneis & Thurman, ×40.

6,7—Polytylites levinsoni, n. sp.; external and internal molds (holotype); ×40.

8–17—Amphissites bradfieldi, n. sp. *8–10*, outer (*8,10*) and inner (*9*) molds of holotype; ×20 and ×40. *11*, outer mold of an instar, complete; ×*20*. *12,13*, inner mold; ×20 and ×40. *14,15*, outer mold, incomplete; ×20 and ×40. *16,17*, outer mold of an instar; ×20 and ×40.

18—Bairdia multihilosa, n. sp. Outer mold of right valve, ×40.

19–21—Glyptopleura cooperi, n. sp., outer mold; ×20 and ×40. *19*, external mold of instar, ×20. *20,21*, external mold of holotype, ×20 and ×40.

22,23—Glyptopleura geissi, n. sp. Inner mold of holotype; ×20 and ×40.

24,25—Turrilepas whithersi, n. sp. Paratype (*24*) and holotype (*25*); ×10.

26,27—Clarkeolepis clarkei, n. gen., n. sp. Holotype (*27*) and paratype (*26*); ×10.

28—Clarkeolepis elegans, n. gen., n. sp. Holotype, ×10.

29—Problematic mold suggestive of a gastropod columella with an *Archimedes*-like core; ×10.

TABLE 2.—LIST OF PELECYPODS AND GASTROPODS FROM BASAL PART OF MILLSTONE GRIT, SCOTLAND

Illustrations and Identifications by Wheelton Hind, 1908	Revised Identification by M. K. Elias, 1950	Closely related to Lower Carbon. British forms	Exclusive local forms	Closely related to American late Mississippian forms
Pelecypoda:				
1. *Palaeolima retifera* (Shumard)	1. *Palaeolima* aff. *simplex* (Phillips)	+		
2, 3. *Aviculopecten regularis* Hind, 1908	2. *Aviculopecten* aff. *clathratus* M'Coy	+		
4. *Aviculopecten neglectus* Geinitz	3. *Aviculopecten* sp.		+?	
5. *Aviculopecten neglectus* Geinitz	4. *Aviculopecten* aff. *losseni* (von Koenen)	+		
6, 7. *Aviculopecten neglectus* Geinitz	5. *Deltopecten* (?) cf. *tahlequaensis* Snider			+
8. *Aviculopecten obliquus* Hind, 1908	6. *Pseudamusium* sp.	+		
9, 10. *Limatulina alternata* M'Coy	7. *Limatulina alternata* M'Coy	+		
11. *Pterinopecten whitei* Meek	8. *Aviculopecten* cf. *stellaris* (Phillips)			+
12. *Pterinopecten whitei* Meek	9. *Aviculopecten* aff. *jonesii* M'Coy	+		
13. *Pterinopecten whitei* Meek	10. *Dunbarella* (?) *carbonaria* Hind	+		
14. *Aviculopecten carbonIferous* Stevens	11. *Limipecten* ? sp.		+?	
15. *Posidoniella laevis* Brown	12. *Posidoniella* (*Caneyella*) cf. *wapanuckensis* Girty			+
16. *Myalina verneuillii* M'Coy	13. *Myalina verneuillii* M'Coy	+		
17. *Nuculana laevistriata* Meek & Worthen	14. *Nuculana intermedia* (R. Etheridge Jr.)	+		
18, 19. *Nucula gibbosa* Fleming	15. *Nucula* cf. *illinoisensis* Worthen			+
20. *Modiola subelliptica* Meek	16. *Modiola* (?) *emaciata* de Koninck	+		
21. *Grammatodon tenuistriata* (Meek & Worthen)	17. *Parallelodon* aff. *semicostatus* (M'Coy)	+		
22, 23. *Protoschizodus curtus* Meek and Worthen	18. *Schizodus depressus* (?) Worthen			+
24–28. *Schizodus wheeleri* Swallow	19. *Schizodus* cf. *batesvillensis* Weller			+
29, 30. *Anthracomya truncata* Hind, 1908	20. *Anthracomya truncata* Hind		+	
31, 32. *Edmondia excentrica* Hind, 1908	21. *Edmondia* aff. *rudis* M'Coy	+		
33. *Edmondia sulcata* Phillips	22. *Edmondia sulcata* Phillips	+		
34. *Edmondia nebrascensis* Geinitz	23. *Edmondia m'coyii* Hind	+		
35. *Edmondia lyelli* Hind	24. *Edmondia lyelli* Hind	+		
36. *Sanguinolites occidentalis* Meek	25. *Allerisma* cf. *walkeri* Weller			+
37, 38. *Sanguinolites occidentalis* Meek	26. *Sanguinolites* cf. *tricostatus* (Portlock)	+		
39. ? *Allorisma reflexa* Meek	27. *Nuculana pandoriformis* (Stevens) Girty			+
40–42. *Tellinomorpha hindii* Bolton	28. *Sanguinolites* (?) sp.	+?		
43, 44. *Solenomorpha cylindrica* Hind, 1908	29. *Solenomorpha cylindrica* Hind		+	
45–47. *Solenomya brevis* Hind, 1908	30. *Solenomya brevis* Hind.		+	
48–50. *Prothyris elegans* Meek	31. *Solen* (*Prothyris*) aff. *meeki* Winchell			+
60, 61. *Solenomya cylindrica* Hind, 1908	32. *Solenomya* cf. *castellata* M'Coy	+		
Gastropoda:				
51. *Loxonema nanum* de Koninck	1. *Zygopleura* cf. *robroystonensis* Longstaff	+		
52. *Naticopsis brevispira* de Ryckholt	2. aff. *Strophostylus carleyana* (Hall)			+
53. *Naticopsis brevispira* de Ryckholt	3. *Holopea* (?) sp.		+?	
55. *Ptychomphalus marcouianus* Geinitz	4. *Pleurotomaria* (?) *subglobosus* Hall			+
56. *Bellerophon marcouianus* Geinitz	5. *Bellerophon torwoodensis* Weir	+		
57, 58. *Euphemus d'Orbignyi* Portlock	6. *Euphemus urei* var. *hindi* Weir	+		
59. *Macrocheilina* sp.	7. *Macrochilina* cf. *altonensis* Worthen			+
	Total Species:	21	6	12

TABLE 3.—PRINCIPAL MEASUREMENTS OF SOME DISCUSSED SPECIES OF *Glyptopleura*

Salem limestone	Length	Height	Length	Height	Redoak Hollow fm.
G. perbella Geis	1.09	.705	.85	.50	*G. warthini*, n. sp.
G. elegantis Geis	.93	.520	.62	.30	*G. geisi*, n. sp.

these with the forms from the basal Millstone Grit cannot be fully denied at the present, it is because the Upper Carboniferous (Pennsylvanian) forms of America have, to a great extent, indigenously evolved from their American Mississippian ancestors, and this relationship is stamped clearly upon their features. We may now properly evaluate the historical importance of Hind's 1908 discovery, even if we must discount as obvious fallacy his assertion that some species of *late* Pennsylvanian age in Nebraska and Illinois occur as migrants in the basal Millstone Grit of Scotland: the latter is, of course, of early Pennsylvanian age. What Hind saw as *Pennsylvanian* affinities are actually affinities with American *Mississippian* forms—thus, the whole picture of migration of these latter forms from America to Scotland at early Millstone Grit age is at once understood and philosophically acceptable.

It would be of some importance now to point out the main evidence in support of the concluded affinities of the basal Millstone Grit invertebrates.

Two corals are identified by Hind, *Zaphrentis omaliusi* M. Ed. & H. and *Densiphyllum charlestonensis* Thom; both forms continued from the Lower Carboniferous of England.

The combined list of identified brachiopods is as follows:

1. *Lingula mytiloides*
2. *Orbiculoidea nitida*
3. *Derbyia* sp.
4. *Chonetes* sp.
5. *Schizophoria resupinata*
6. *Productus* cf. *longispinus*
7. *?Spiriferina cristata*
8. *?Seminula ambigua*
9. *Pugnax pugnax*

These incomplete identifications indicate some definite affinities with the European Lower Carboniferous forms. No attempt is made by Hind to find American affinities for any of these forms, though he must have been tempted to do so in view of his strong belief that the pelecypods and gastropods show such affinities. Hind emphasizes local Lower Carboniferous relationships of these brachiopods, pointing out that *Schizophoria resupinata* Morton continued upwards from the local uppermost Lower Carboniferous.

Hind identified only one cephalopod in the fauna which he doubtfully refers to *Glyphioceras phillipsi* Foord & Crick (Hind, 1908, p. 333), a British species.

One scaphopod was described by him: *Entalis meekianum* Geinitz (Hind, 1908, p. 355, pl. 2, fig. 54), but its specific identification can be accepted only as provisional.

Hind's list of original identifications of pelecypods and the list of reidentification of the same forms are entered in Table 4. The

TABLE 4.—PRINCIPAL DIMENSIONS OF SOME DISCUSSED SPECIES OF *Kirkbya*

Species	Stratigraphy	Location	Length	Height
K. bendensis	Seville	Illinois	.97	.49
K. bendensis	Fulda	Illinois	.82	.43
K. bendensis	Upper Morrow	Ardmore, Okla.	.90	.40
K. bendensis	Johns Valley	Oklahoma	.90	.44
K. bendensis	Redoak Hollow	Ardmore, Okla.	.90	.41
K. intermedia	Kinkaid	Illinois	.83	.42
K. symmetrica	Kinkaid	Illinois	.78	.42
K. elongata	Paint Creek	Illinois	.87	.37

order of the entries is the same as that by Hind for the sake of convenient reference to his illustrations; the number of his figures are entered at the left side. The different figures in the list of reidentified forms are put merely for the convenience of count. Among the pelecypods of undoubted American affinities the following forms seem most important:

(1) *Solen* (*Prothyris*) aff. *meeki* Winchell, also singled out as important evidence of this affinity by Hind (1908, p. 332,353). Although one species of this genus, *Prothyris bergica* is known from the lowest Carboniferous of Germany (Drevermann, 1902, p. 498, pl. 14), the genus is eminently American, ranging from the Upper Mississippian (Waverlian) to the Upper Pennsylvanian (Virgil), where it could have migrated from western Europe at the end of early Mississippian time. The form which Hind describes and illustrates in some detail is, indeed, much like American species *elegans*, but may also be easily identified with its predecessor *meeki* from the Waverlian, or with the Redoak Hollow representative of this genus, here placed in sub-generic rank to the living genus *Solen*. The most characteristic feature of *Prothyris* is the notch in the antero-ventral part, caused by the linear sinus that separates an anterior wing from the rest of the shell. This notch is smaller (or lower in relation to the ventral edge) in Mississippian as compared with Pennsylvanian species, and its position in Scottish form, illustrated by Hind (1908, pl. 2, figs. 48–50) is intermediate between that in normal Mississippian and normal Pennsylvanian forms.

(2) Hind identified *Caneyella wapanuckensis* Girty as *Posidoniella laevis* Brown. This identification was sufficiently good at his time because Girty established his genus *Caneyella* for some pelecypods in the Caney shale of Oklahoma in 1909 (p. 32). In his description of *Caneyella* Girty admits that he has "for some time had the shells under consideration assigned" to *Posidoniella*, and only later decided to erect for them a new genus *Caneyella* on the evidence of "lobe-like character of the anterior auricle" and "acuminate prolongation of the posterior wing, a difference which may be trivial but which I believe is not without its significance" (Girty 1909, p. 34). In *C. wapanuckensis*, to which Hind's single illustrated specimen seems very closely related, Girty sees another feature, "the large basal aperture—which is wanting in *Posidoniella*" (ibid., p. 34). However, it seems that *Caneyella* is so close to *Posidoniella* that it can be considered as its subgenus, rather than a genus.

The third pelecypod whose American affinities seem certain is Hind's *Nucula* (1906, pl. I, figs. 18,19), which he identified with *Nucula gibbosa* Fleming from the upper part of the Lower Carboniferous of England. It differs from the latter, however, by narrower, sub-acuminate umbones, which are directed more nearly upwards than forwards; the points of the umbones are proportionally farther from the anterior margin, and the shell is only 5 mm. long, or about one-third of the average specimens of *N. gibbosa*. In all these respects it is much more like *Nucula illinoisensis* Worthen from the St. Louis limestone of Illinois (Worthen, 1890, p. 198, pl. 19, figs. 4,4a) and Pitkin limestone of Arkansas (Easton, 1942, pl. 10, fig. 2), the latter being only 1½ as large as *Nucula* from the basal Millstone Grit, and having similarly acuminate umbones.

Among other pelecypods, perhaps the two reidentified species of *Schizodus* can be most reliably compared with our late Mississippian species of the genus, while the remaining pelecypods of American affinity seem to be closer to the known Mississippian forms of American rather than to European Lower Carboniferous forms.

Among seven species of gastropods described by Hind four display decided American affinities, making an even higher percentage of such forms among the gastropods than among the pelecypods. This is an even stronger indication of such affinity than appeared to Hind.

As the present analysis of the molluskan fauna from the Scottish basal Millstone Grit is based only on Hind's illustrations and descriptions, and not on examination of his originals, it would be presumptuous to expect that no possible error in identification will be corrected in the future, because some of his drawings or descriptions may not be as accurate or complete as desired. Additional discoveries may be expected in the lower Carboniferous of both America

and Europe which will necessitate revision of the present identifications. However, it seems that some of the forms in the present analysis and in that previously made by Hind are correctly interpreted as indicative of American affinities. Thus we have good reason to conclude that some American late Mississippian forms migrated to Scotland at the end of Early Carboniferous (Mississippian) time. This conclusion appears probable because independent analysis of different groups of pelecypods and gastropods identified in the Redoak Hollow fauna are here shown to be reciprocal migrants to America from the British Isles at about the same time. The end of Lower Carboniferous or Mississippian time was apparently the time when marine connection between Western Europe and south central North America became so well established as to permit the most mobile among the invertebrates, such as pelecypods and gastropods to migrate in both northeastward and southwestward directions. The fact that at the same time some ammonoids, such as *Eumorphoceras*, became common to both English and American seas has already been established. Similar relationships is now indicated for the other mollusks. The cumulative evidence may be utilized in making more precise correlation of the principal events at the close of Mississippian time in America and western Europe. The position of American molluskan migrants is very close to the base of the Scottish Millstone Grit, and only a few feet below the horizons where, according to Kidston, the Lower Carboniferous land flora makes its last appearance in the local geological sequence. It might be roughly approximated that it took as much time for British mollusks to migrate southwestward and reach southern Mid Continent, as it took the American mollusks to migrate from the latter area northeastward to reach Scotland. If so, the Redoak Hollow, where these British mollusks are found, can be properly correlated with the basal part of the Millstone Grit of Scotland, or somewhere in the Namurian.

With this paleontologic and lithologic correlation in mind, we may attempt to establish the correlation of diastrophic movements at the end of early Carboniferous time. Detailed stratigraphic and paleontologic work by British geologists enabled them to establish a series of orogenic movements classified as Sudetian. According to Hudson and Mitchell (1937) the three most conspicuous of these movements can be distinctly recognized, and they are placed by them (1) at the end of Middle Visean or zone D_1 (=B), (2) at the middle of Upper Visean, or the horizon between zones P_1 and P_2 (within zone D_2), and (3) at the end of Upper Visean or zone D_2, or slightly higher (between subzones E_{1a} and E_{1b} of zone D_3) respectively.

If the correlation of the mass migration of mollusks between the British Isles and the American Mid-Continent is correct, then we may also accept a correlation of these Sudetian movements with the American movement that uplifted the Ouachita and provided coarse clastics for the Redoak Hollow and the later sandstones in the Springer.

In the light of the new understanding of the interrelationship of mollusks in Scottish and American seas at the end of Mississippian time, a new understanding of the behavior of the other invertebrates may also be attempted. Most important of these are the sedentary groups, such as corals, crinoids (and cystoids), bryozoans, and brachiopods. The present record from the Redoak Hollow shows that crinoids, bryozoa, and brachiopods in this sedimentary series do not differ substantially from the forms common in the late Mississippian series of southern Mid-Continent and of the Upper Mississippi region. A greater change in these invertebrate groups came about at the initiation of Morrow time. It seems that even the incomplete information on corals and brachiopods accompanying the mollusks in the basal part of the Millstone Grit of Scotland is sufficient to show that these sedentary invertebrates in British seas behaved much like the crinoids, bryozoans, and brachiopods of the Mid-Continent. They too continued on without any appreciable change from the Lower Carboniferous or Avonian below to the Millstone Grit or Namurian above. In the British Carboniferous, too, corals and brachiopods do not provide any appreciable supplementary paleontologic evidence that would support a major paleontologic break at the end of

Lower Carboniferous (Avonian) time. The latter is manifested only by an appreciable change in the mollusks and terrestrial plants. In both America and the British Isles the sedentary invertebrates tended to preserve their corresponding Mississippian and Avonian aspects into Redoak Hollow and Namurian times correspondingly, while the mollusks became rejuvenated by migrants from the corresponding Lower Carboniferous seas. The mollusks furnished the first wave or vanguard of typical Pennsylvanian population in America, and typical Upper Carboniferous population in Europe; while the less mobile, sedentary invertebrates acquired their Pennsylvanian (and Upper Carboniferous) aspect only at a somewhat later time, which, in America, is called Morrow. This latter change is manifested differently in western Europe, where a continental regime with swampy vegetation was established soon after the initiation of Millstone Grit or Namurian time, as is also the case in the Appalachian region of America.

SCAPHOPODA

Genus *Laevidentalium*

LAEVIDENTALIUM sp. cf. L. VENUSTUM (Meek & Worthen)

Pl. 3, fig. 1

1861. *Dentalium venustum.* MEEK & WORTHEN, Acae. Nat. Sci. Phila., Proc., p. 145.
1866. *Dentalium venustum.* MEEK & WORTHEN, Ill. Geol. Survey, Rept., v. 2, p. 284, pl. 19, fig. 8.
1903. *Plagioglypta venusta.* GIRTY, U. S. Geol. Survey, Prof. Paper no. 16, p. 453.
1909. *Laevidentalium venustum.* GIRTY. U. S. Geol. Survey, Bull. 377, p. 41–42, pl. v, figs. 5,5a.

The largest fragment of this species is 9 mm. long, with diameter 1.5 mm. at distal end and .7 mm. at proximal end. The conch is straight and almost smooth, with only faintly visible few and irregularly distributed transverse striae. Near the proximal end instead of striae are gentle, broadly spaced annulations, about 3 per 1 mm.: the annulations are very gently convex, separated one from another by narrow and shallow grooves. This feature has not been recorded for *L. venustum* and, if proved a constant feature, may be considered sufficient for recognition in the form from the Redoak Hollow a new variety of *L. venustum* or even a new species.

Genus PLAGIOGLYPTA

PLAGIOGLYPTA ANNULOSTRIATUM (Meek & Worthen)

Pl. 3, fig. 2

1870. *Dentalium ? annulostriatum.* MEEK & WORTHEN, Acad. Nat. Sci. Phila. Proc., p. 45.
1873. *Dentalium ? annulostriatum.* MEEK & WORTHEN, Ill. Geol. Survey, v. 5, (Paleontology), p. 589–590, pl. 29, fig. 7.
1903. *Plagioglypta annulistriata.* GIRTY, U. S. Geol. Survey Prof. Paper 16, p. 452.
1915. *Plagioglypta annulistriata.* GIRTY, U. S. Geol. Survey Bull. 544, p. 147–148, pl. 25, figs. 15–16a.

Several incomplete specimens compare satisfactorily with Meek and Worthen species. A typical fragment is 5.5 mm. long, with 1.5 mm. diameter at the wide end, and 1 mm. at the narrow end. The conch is gently curved, and ornamented by slightly oblique transverse costae. Costae are denser in the narrow proximal end, 15 per 1 mm.; then grow gradually large, and are spaced 9 to 10 per 1 mm., when diameter is more than 1 mm. and less than 1.5 mm.; and at 1.5 mm. diameter the spacing is 7 per 1 mm. The costae are somewhat more uniform in size and spacing than those in the example from the Wewoka illustrated by Girty on fig. 16, pl. 25, 1915. The form from the Redoak Hollow is unlike *P. meekiana*, whose similar transverse ornamentation is faint to obscure.

CEPHALOPODA

Genus CYCTOCERAS

CYCLOCERAS RANDOLPHENSIS Worthen

Pl. 3, figs. 7,8

1861. *Orthoceras annulo-costatum.* MEEK & WORTHEN, Proc. Acad. Nat. Sci. Phila., p. 147.
1866. *Orthoceras annulo-costatum.* MEEK & WORTHEN, Ill. Geol. Survey, v. 2, Paleontology, p. 304–305, pl. 24, figs. 3a,3b.
1909. *Cycloceras randolphensis.* GIRTY, U. S. Geol. Survey Bull. 377, p. 48.
1911. *Orthoceras randolphense.* MORSE, Proc. Ohio Acad. Sci., v. 5, p. 415, fig. 35.
1915. *Cycloceras randolphensis* (?). SNIDER, Okla. Geol. Survey, Bull. no. 24, p. 119.

The single specimen referable to this species is represented by both external and internal molds of a fragment about 9–10 mm. long, and about 25 mm. in diameter

(estimated). The prominent costae (annulations) of the specimen are about 1.5 mm. wide, and 6.5 mm. from crest to crest apart, there being therefore four of them in a space equalling the diameter. This spacing is very characteristic of *C. randolphense*, and the specimen from the Redoak Hollow resembles very much the original illustration of *Orthoceras angulo-costatum* from the Chester of Illinois (Meek and Worthen, 1866, pl. 24, fig. 3a), matching particularly the uppermost (distal) part of it, where the shell is rapidly expanding. The specimen from the Redoak Hollow is very distinctly transversely costate on the outside of the shell, the fine and very narrow costae being irregularly spaced, from 4 to 10 per 1 mm. There are fine transverse striae on the just mentioned sketch by Meek and Worthen, but they are shown more distantly spaced, about 2 per 1 mm.; however, perhaps they have been sketched only approximately, as in the text (p. 365) they are referred to as mere "traces of fine transverse striae," and no observation of their spacing is given. Thus, until future comparative investigation of the form from the Chester discloses any differences, the form from the Redoak Hollow may be considered conspecific with it.

CYCLOCERAS MEEKI, n. sp.
Pl. 3, figs. 3–6

Several external and internal molds collected mostly at locality 3, some at loc. 4. Conch cylindrical, circular in cross-section, tapering imperceptibly, largest diameter to about 20 mm. Conch annulated, prominent transverse costae slightly narrower than the gently concave spaces between them. 4 to 5 annulations per 10 mm. at 10 to 12 mm. conch diameter (figs. 3–5); 3 per 10 mm. when diameter approaches 20 mm. (fig. 6) Fine transverse irregularly spaced costae cover ribs and spaces between them, 4 to 10 per 1 mm.

Discussion.—In the prominence of the transverse costae and their spacing *Cycloceras meeki* is close to *Protocycloceras* (?) *rushense* (?) from the Wewoka of Oklahoma described and illustrated by Girty (1915, p. 235–236, pl. 27, figs. 9–10b). However, the two differ greatly in shape of conch, which is practically cylindrical with only very insignificant tapering in *C. meeki*, while in *P. rushense* the conch tapers rapidly and hence is called by Girty "conical." *Cycloceras randolphensis* differs in fewer annulations and oval cross-section.

Genus STROBOCERAS Hyatt 1884 (emend. 1893)

STROBOCERAS FURNISHI, n. sp.
Text-figs. 5,6; Pl. 3, fig. 9

Description.—Single septate fragment of a whorl at about 4 mm. radius (at its distal end), or about 7 mm. diameter. Septa from .3 to .6 mm. apart at 3.5 mm. radius, to 1 mm. apart at 4 mm. radius. Spongy matrix of mold in this part of fragment crushed out in preparation to reveal outer mold with well preserved sculpture. Cross-section of volution about as wide as high, sharply angular because of several concentric ribs with unequal concave bands between them. Lateral band slightly wider than all others, with sharp transverse (radial) curved ribs slanting in antero-ventral direction, and multiplying by intercalation. Lateral band flanked on both sides (ventral and dorsal) by very narrow band followed by wider band. Siphuncle near venter at a distance about $\frac{1}{4}$ of height of volution. Maturity of volution indicated by broadly convex outline of dorsal side (connected to inner volutions).

Discussion.—The comprehensive review of the genus and species of *Stroboceras* by Miller and Garner (1953) indicates that none of the species has the transverse outline of volution similar to *S. furnishi*, but it is nearest to *S. hartii* (Dawson), the genotype (see Miller and Garner, 1953, text-fig. 6-A on p. 136) from the upper Mississippian Windsor limestone of Nova Scotia.

The upper Mississippian (Ste. Genevieve) form whose fragment was described by Weller as *Stroboceras* sp. (1916, p. 263, pl. 19, fig. 16) and compared with *S. sulcatum* (Sowerby) is apparently more like this species than *S. furnishi*, as Weller described it "laterally flattened, disk-like." *S. sulcatum* is described from the Mississippian of Kentucky by Miller and Furnish (1940, p. 359, text-fig. 3, pl. 45, figs. 8,9), and believed to be Meramec in age. Its cross section is quite different from *S. furnishi*.

Genus EUMORPHOCERAS Girty
EUMORPHOCERAS GIRTYI Elias
Text-figs. 7,8; Pl. 3, figs. 10–13

pars 1909. *Eumorphoceras bisulcatum*, GIRTY, U. S. Geol. Survey Bull. 377, p. 68–70, pl. 9, figs. 16–16b only.
pars 1948. *Eumorphoceras bisulcatum*, CLOUD & BARNES, Texas Univ. Bull. 4621, p. 53, 237, pl. 44, figs. 33–35.
pars 1948. *Eumorphoceras bisulcatum*, MILLER & YOUNGQUIST, Jour. Paleontology, v. 22, p. 662–665, pl. 100, figs. 13–17 only.
pars 1949. *Eumorphoceras bisulcatum*, YOUNGQUIST, Jour. Paleontology, v. 23, p. 299–301, pl. 58, fig. 4 only.
1956. *Eumorphoceras girtyi*, ELIAS, in Petroleum Geology of Southern Oklahoma, Am. Assoc. Petroleum Geologists, p. 130–132, pl. 6, fig. 7.

Description.—Two juvenile shells collected at locality 3. Larger shell 5 mm. diameter and nearly 3 mm. wide, the inner mold with distinct ventral groove (pl. 3, fig. 12) corresponding to intra-ventral carina. Conspicuous curving lateral ribs 10 per volution. Distinct constriction at 4 mm. diameter in the larger specimen (pl. 3, fig. 10). Very young conch with transverse ribs on its umbilical slope of the second volution is provisionally referred to *E. girtyi* (Text-figs. 7,8).

Discussion.—The presence of intra-ventral carina and a constriction are characteristic for *E. girtyi*, and together with smaller number of lateral ribs distinguish it from *E. bisulcatum sensu stricto*. The presence of the species in the Redoak Hollow indicates early Namurian (E_1) age for the formation.

CRAVENOCERAS sp.
Pl. 3, figs. 14,15

Two small fragments of dorsal part of a conch, one with external sculpture preserved, and the other with suture line, are comparable to *C. richardsonianum*. It has an ecologic and even stratigraphic interest because of the enigmatic small circular "pock-marks" upon the shell, and which are described below as *Cyclopuncta girtyi*, n. sp. Previously, exactly the same kind of marks and in a similarly scattered fashion, were discovered by Girty (1909, p. 53, pl. 6, fig. 6) on the conch of another cephalopod *Bactrites* (?) *smithianus* Girty, found in association with *Crevenoceras richardsonianum* in the Caney shale. It seems that the new find of the combination of *Cravenoceras richardsonianum* with the punctae of *Cyclopuncta girtyi* suggests that the previously recorded occurrence of these punctae on *Bactrites* (?) made at collection station 2083, in the "Caney shale (lower part of shaly portion)" Tishomingo quadrangle, center of north side of sec. 14, T. 2 S., R. 7 E. (Girty, 1909, p. 74, and explanation to Pl. 6, fig. 4a) belongs in the part of the Caney stratigraphically approximating the Redoak Hollow.

After the above description has been completed additional fragment of the species was discovered that has the main part of suture preserved on the internal mold. This discovery fully confirms the existence of *Cravenoceras richardsonianum* in the Redoak Hollow. The preserved part of the suture, which consists of the ventral or siphonal saddle, with a slight sag at the top, a narrow siphonal lobe, broadly rounded first lateral saddle, and an angular lateral lobe—is quite comparable in general design and size to the corresponding part of the suture of 24 mm. diameter adult *C. richardsonianum* illustrated by Girty (1909, pl. 11, fig. 4). The external sculpture preserved on the outer mold of this fragment consists of distinct narrow transverse ridges, 3 to 4 of which can be counted per 2 mm. across, just as in Girty's types.

CRUSTACEA
TRILOBITA
PHILLIPSIA (?) sp.

The single fragment of the pigidium of a trilobite is so incomplete as to preclude specific identification, and even generic assignment is quite provisional.

OSTRACODA
Family APARCHITIDAE Jones, 1901
Genus PARAPARCHITES Ulrich & Bassler
PARAPARCHITES (?) sp. cf. P. ELONGATUS Bradfield
Text-fig. 18

1935. *Paraparchites elongatus*. BRADFIELD, Bull. Am. Paleontology, v. 22, p. 32; pl. 1, fig. 3.

Only one internal mold of a right valve was recovered, and identification of this simple, unornamented species on the strength of this mold can be only provi-

sional. However, in view of the fact that it corresponds well in outline to the single illustrated right valve of the original description, is about the same size, and occupies a not very much earlier stratigraphic position—the indicated identification seems justifiable.

The original from the Otterville is a rare form, .63 mm. long; the single specimen from the Redoak Hollow is about .8 mm. long.

Family KLOEDENELLIDAE Ulrich & Bassler, 1908
Genus SANSABELLA Roundy
SANSABELLA sp. cf. S. TRUNCATA Cooper
Text-figs. 36,39

1941. *Sansabella truncata.* COOPER, Ill. Geol. Survey, Rept. Inv. no. 77, p. 60–61, pl. 13, figs. 36–41.

The species is represented by one well preserved left valve of a normal specimen (with left valve overlapping the right valve), but only interior of the valve is exposed for study. The example from the Redoak Hollow belongs undoubtedly to the group of small species of *Sansabella* well represented in the Chester, particularly lower Chester, but only one species is registered by Bradfield in the Pennsylvanian of Ardmore, being stratigraphically high in the local section (Hoxbar). However, should we accept in the same genus and species both sinistral and dextral forms, and thus place in the same species *Sansabella whitei* Bradfield and *Kirkbyina laevis* Warthin, which according to Bradfield are identical, except one being "a mirror image of the other" (Bradfield, 1935, p. 44)—a nearly continuous record of *Sansabella* in the Ardmore Basin is thus lowered to the Redoak Hollow. Bradfield records *Kirkbyina laevis* from the base of the Dornick Hills to the Hoxbar. If we admit some variation in outline of a shell within a species, it would be natural to include the present example from the Redoak Hollow in *Sansabella laevis* (Warthin). However, if the presence of well developed node in the upper posterior angle has any taxonomic significance, the present form from the Redoak Hollow should be classified rather with *Sansabella truncata* Cooper, although the latter is recorded only from the Golconda. The form from the Redoak Hollow matches it well except its length is slightly smaller (.65 mm.), being in this respect more nearly like that in *Sansabella vinitaensis* (Harlton) of the Fayetteville of Arkansas and the Renault of Illinois. Thus the present form in the Redoak Hollow combines the features of the lower Chester forms and is less like any of the described forms from the upper Chester. The examples of *Sansabella laevis* (Warthin) described by Bradfield are longer than the present form from the Redoak Hollow, as they measure .73–.75 mm. in length.

SANSABELLA KESLINGI, n. sp.
Text-fig. 35

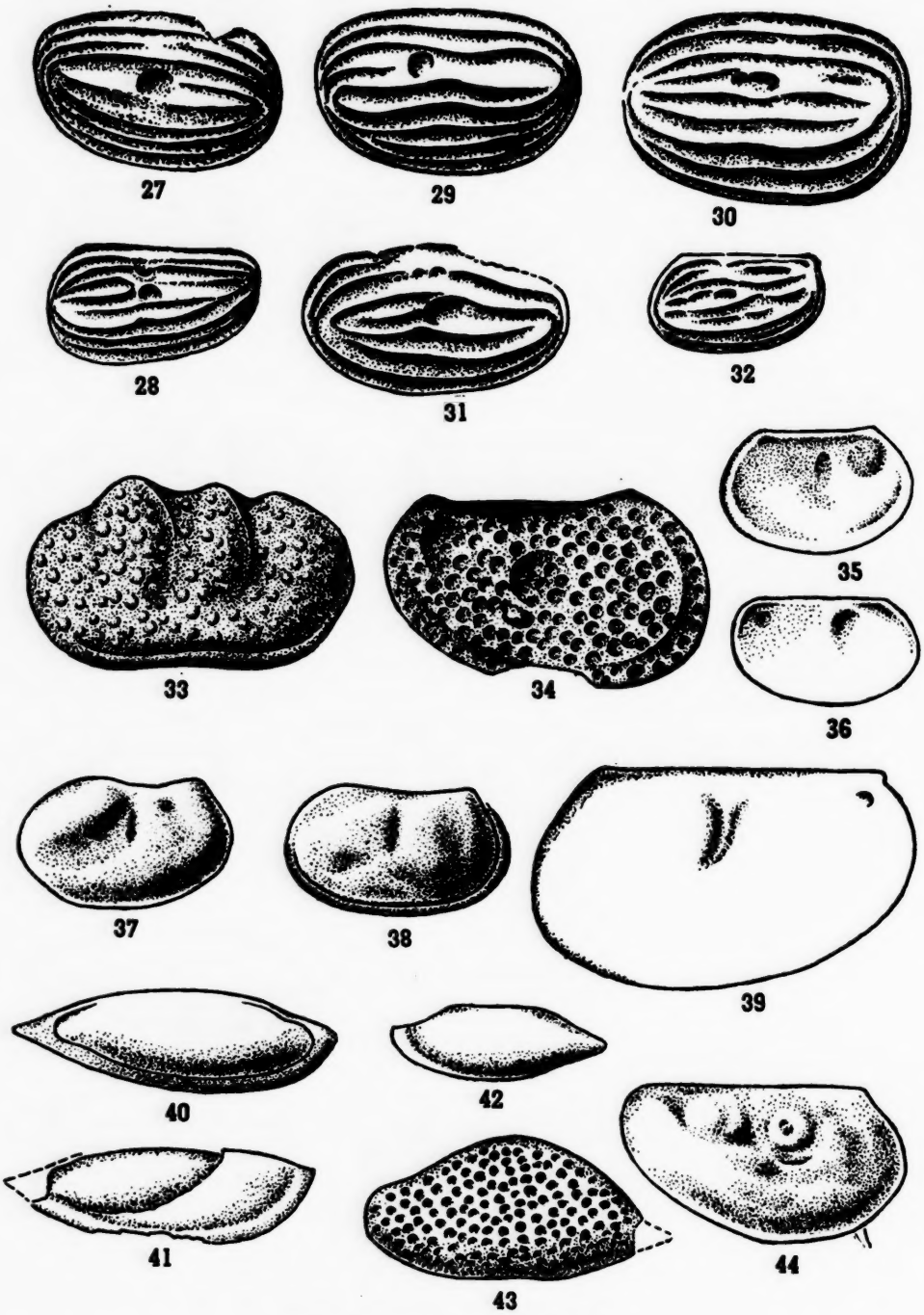
The only specimen on which this new species is based is a complete external mold of left valve. Its most characteristic features are a broad circular depression in anterodorsal corner of the valve, and a short spine at posterior end of the straight hinge line. The valve is subovate, with greatest height anterior to the center, slightly more so than the deep pit-like sulcus. The edges of valve are about equally depressed all way around except antero-dorsal part where the above mentioned circular depression is located, and above which the end of hinge is slightly produced into a cusp. The valve is about .70 mm. long and about .41 mm. high.

S. keslingi is perhaps nearest to *Sansabella bradfieldi* (Coryell & Sohn) in that the latter too seems to possess a wide anterodorsal depression (see particularly Cooper, 1941, pl. 13, figs. 47,48), but differs from it in smaller size, development of posterior spine, and different form ratio: its length/height ratio is 1.7, while that of *S. bradfieldi* varies from 1.51 to 1.55 (Cooper, 1941, p. 59).

SARGENTINA sp. cf. S. ALLANI Coryell & Johnson
Text-figs. 37,38

1939. *Sargentina allani,* CORYELL & JOHNSON, Jour. Paleontology v. 13, p. 223, pl. 25, fig. 9.
1941. *Sargentina allani,* COOPER, Ill. Geol. Survey Rept. Inv. no. 77, p. 38, pl. 6, figs. 19–22.

The species is referred to *Sargentina* on the evidence of its arcuate dorsum and the character of sub-central depression, which



EXPLANATION OF TEXT-FIGS. 27–44

FIGS. *27,28—Glyptopleura warthini*, n. sp. ×40. *27*, inner mold of right valve (holotype). *28*, inner mold of left valve of instar.

is "a single dimple drawn out into a distinct sulcus in the dorsal half,"—see characteristic of the genus (Coryell & Johnson, 1939, p. 223). Also, the right valve is obviously the larger and overlapping in *S. allani*, as per definition of the genus. According to Cooper, however, reversal of valve in this respect is a normal phenomenon within a genus and species, as he observed, for instance on a number of specimens of *Sansabella bradfieldi* (Cooper, 1941, p. 59). Thus he refers to *Sargentina allani* Coryell and Johnson his specimens from the Clore of the Chester series, which have left valve larger and overlapping the right valve. Also, Cooper considers *S. forsetii* (Coryell & Johnson, 1939, p. 224, pl. 25, figs. 10a,b) a female of *S. allani* (*ibid.*, p. 223, pl. 25, figs. 9a,b,c); he also describes the new species of the genus, *S. asulcata* from the Kinkaid of Illinois (Cooper, 1941, p. 39, pl. 6, figs. 1,2) and transfers to this genus *Sulcella crassimarginata* Croneis & Thurman (1938, p. 328, pl. 7, figs. 15,16), also from the Kinkaid.

The length of this form from the Redoak Hollow is circa .73–.75 mm., which is practically the same as in *S. crassimarginata* (.75 mm.), but it differs from the latter in a more arcuate dorsum and a more nearly central position of the sulcus. The dorsum in *S.* cf. *allani* is more pronouncedly arcuate than in any previously known species of the genus, and the specimens of *S. allani* illustrated by Cooper (1941, pl. 6, figs. 20,22) are nearest to it in this respect; but the latter species is larger (.91–.95 mm. long) and its sulcus is much closer to anterior than to posterior. Besides the most pronounced arcuation of the dorsum, another distinctive feature in *S.* cf. *allani*, is a small but distinct diagonal ridge at the crest of the elevation anterior to the sulcus. The posterior in all three internal molds of the left valve referred to the species is only very slightly thinner than the anterior, all shells being probably male.

Genus CARBOPRIMITIA Croneis & Funkhouser

CARBOPRIMITIA sp. cf. C. ROTUNDA Croneis & Funkhouser

Text-fig 17

1939. *Carboprimitia rotunda*, CRONEIS & FUNKHOUSER, Denison Univ. Sci. Lab. Bull., v. 33, p. 338, pl. 9, figs. 3,4.

pars 1941. *Carboprimitia rotunda*, COOPER, Ill. Geol. Survey, Rept. Inv. no. 77, p. 63, pl. 14, figs. 26–29.

The single internal mold of a right valve is referred to genus *Carboprimitia* with considerable degree of confidence, most characteristic for the genus being the presence of an early developed ventral border in the valve (see Croneis & Funkhouser, 1939, p. 336, where the diagnosis of their genus *Carboprimitia* is given). On the other hand, the specific reference of the form from the Redoak Hollow to *C. rotunda* is uncertain because it differs from the illustrated carapaces of the latter species by more nearly central position of the pit and its smaller size. As to the general outline of the valve from the Redoak Hollow it seems nearest to *C. rotunda* from the Clore (Cooper, 1941, pl. 14, fig. 16) than to the other Chester species of the genus illustrated by Cooper, but in proportion of length to height it is

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←

29,30—Glyptopleura cooperi, n. sp. *29*, inner mold of left valve; ×35. *30*, inner mold of left valve (holotype); ×40.
31—Glyptopleura scotti, n. sp. Inner mold of left valve; ×50.
32—Glyptopleura geissi, n. sp. Inner mold of left valve; ×40.
33—Polytylites coryelli, n. sp. Inner mold of right valve; ×80.
34—Polytylites kellettae, n. sp. Outer mold of right valve; ×100.
35—Sansabella keslingi, n. sp. Outer mold of left valve; ×40.
36,39—Sansabella sp. cf. *S. truncata* Cooper. *36*, outer mold of left valve; ×40. *39*, outer mold of right valve; ×80.
37,38—Sargentina sp. cf. *S. allani* Coryell & Johnson. Inner molds of right valves; ×40.
40,41—Bairdia billjohnsoni, n. sp. ×40. *40*, inner mold of right valve. *41*, inner mold of right valve with part of shell adherent to it (holotype).
42—Bairdia croneisi, n. sp. Inner mold of left valve; ×40.
43—Bairdia multihilosa, n. sp. Outer mold of right valve; ×40.
44—Nuferella rothi, n. sp. Inner mold of right valve; ×80.

nearest to *C. longula* Cooper (1941, pl. 14, fig. 26). Perhaps the form from the Redoak Hollow should be considered a new species, that would be characterized by a central position of the comparatively small pit, its proximity to the dorsal edge, and the elongated shape of the valve. On the other hand it seems prudent not to introduce a new name for this species on the evidence of a single mold of its right valve alone.

Position of pit only slightly anterior to the center of carapace is illustrated for *Carboprimitia rotunda* from the Clore (Croneis and Funkhouser, 1939, pl. 9, fig. 3; also Cooper, 1941, pl. 14, figs. 16,19), and a seemingly even more nearly central position is occupied by the pit in the right valve of *Carboprimitia simulans* (from the Kinkaid, Croneis and Thurman, 1939, pl. 7, fig. 25). Cooper records *C. rotunda* upwards to and including the Kinkaid, but does not illustrate its representative from the Kinkaid. The length of all discussed forms of *Carboprimitia*, including that from the Redoak Hollow is 1 mm. or slightly longer.

Genus NUFERELLA Bradfield
NUFERELLA ROTHI, n. sp.
Text-fig. 44

This is the third species of the genus *Nuferella*, which was originally established on a single and rare species *Nuferella infrequence* Bradfield from the Hoxbar formation (and possibly also from the Deese) of Ardmore (Bradfield, 1935, p. 45–46, pl. 3, fig. 4a,b). Subsequently, Coryell & Sohn described another species *N. wellsi* from the top of the Reynolds member of the Mauch Chunk shale of West Virginia, which they correlate with the upper part of the Chester (1938, p. 601–602, pl. 69, fig. 9).

At least two internal molds, one of right and the other of left valve were recovered from the Redoak Hollow. They show all essential features of the genus: subrhomboidal outline; with distinct forward swing; long, straight hinge line; anterior height much greater than posterior height; prominent central sulcus, bordered by two unequal elevations one posteriorly and the other anteriorly; and a small tubercle near posterior end of hinge line. The new species differs from both previously described species by relatively more prominent posterior elevation but is more near Pennsylvanian genotype than the Mississippian species in its elongated outline and practically same size (*N. wellsi* is larger, being .6 mm. long).

Nuferella rothi is about .5 mm. long and .25 mm. high in the anterior, which dimensions are about same as in *N. infrequence* (.48 and .27), though with slight tendency toward greater elogation in *N. rothi*.

Genus JONESINA Ulrich & Bassler
JONESINA sp. cf. J. SPINIGERA Cooper
Text-fig. 16

1941. *Jonesina spinigera*. COOPER, Ill. Geol. Survey, Rept. Inv. no. 77, p. 57; pl. 12, figs. 16–17.

The single recovered outer mold of right valve is so much like the left valve (in reverse) of *J. spinigera* illustrated by Cooper as to leave no doubt in their close relationship. Identical are the general outline and principal dimensions, straight hinge, shallow subcentral sulcus between two principal humps located near dorsal edge, pitted surface, and short anterior and posterior spines just under the ends of the hinge. Although only approximately established on the mold with slightly ragged edges the length and height of right valve (.65 by .40) are remarkably close to Cooper's measurements for *J. spinigera:* .64 by .39 mm. The only differences which seem to indicate at best only varietal rank of the form from the Redoak Hollow are (1) slightly greater anterio-ventral truncation, which makes its anterior more nearly wedge-shaped; (2) slightly retreated position of the anterior spine, which places it at the antero-dorsal edge of the anterior hump, instead of at the anterior end of the hinge, as in the holotype from Paint Creek formation; (3) presence of a small spine in postero-ventral part of the valve, a feature not mentioned for *J. spinigera* by Cooper.

Cooper collected *J. spinigera* in Paint Creek and Golconda formations of the Chester in Illinois, and questionably also in Menard formation; but does not illustrate the specimen from the latter. The present identification extends upward the stratigraphic range of the species, and future finds may determine whether the above mentioned slight differences between the cara-

paces from the Redoak Hollow and the Paint Creek are of any evolutionary significance.

Genus DELOIA Croneis & Thurman, 1938

The genus *Deloia* was introduced by Croneis & Thurman (1938, p. 301) for a group of *Jonesina*-like Chester ostracodes characterized by a straight hinge line and "*Knoxina*-like outline, and serrated flanges along carapace outline"; it possesses an anterior sulcus, and its right valve overlaps left. Species of the genus were found throughout Chester group, from Renault limestone to the Kinkaid, all described by Croneis and his associates. When Cooper monographed all Chester ostracodes he published several new illustrations of *Deloia*, but did not discuss this genus and limited himself to much abbreviated description of only two out of four illustrated species, one of which was newly introduced by him (*D. tumida* from the Kinkaid). Nevertheless he contributed much to the understanding of the genus by the photographs of the specimens which are better preserved and hence show more detail than those previously described. Thanks to this it is now possible to point out that in the form from the lower horizons of the Chester a more or less conspicuous dorso-lateral spine, just next to the sulcus, is invariably developed; but in the species from the Clore and higher in the Chester the spine becomes inconspicuous or even fades out entirely. Hence it seems that presence of this spine is of considerable specific and stratigraphic significance, and because of that the specimen of *Deloia sulcata* from the Golconda which Cooper illustrates is not considered here to be identical with this species whose original is from the Clore, and in which Croneis and Funkhouser (1938) describe no spine, though their photograph (pl. 9, fig. 18) does show an indication of a dorsal, slanting platform posterior to the sulcus, which occupies the same position as the elongated slanting spine in the discussed specimen from the Golconda. Indeed, one could suppose, as perhaps Cooper did, that the spine in his specimen has been merely eroded—but the present find of the same species, *Deloia sulcata* in the Redoak Hollow, whose surface is perfectly preserved, even if in form of external mold, shows no trace of spine, while it does show the presence of platform-like swelling, much as in the type of *D. sulcata* from the Clore.

DELOIA SULCATA Croneis & Funkhouser
Text-fig. 13

1938. *Deloia sulcata*, CRONEIS & FUNKHOUSER, Denison Univ. Sci. Lab. Bull., v. 33, p. 344–345, pl. 9, fig. 18.

not 1941. *Deloia sulcata*, COOPER, Ill. Geol. Survey, Rept. Inv. no. 77, pl. 11, figs. 46–48.

Two specimens of this form have been recovered from the Redoak Hollow, but only one specimen, which is right valve, is practically complete, being represented by both external and internal molds. Its size and proportions are exactly as in the type specimen of *D. sulcata*, and in addition it has its external surface in better preservation than can be seen on Croneis and Funkhouser's single photograph (1938, pl. 9, fig. 18). Although they omit to state whether the surface is smooth or not, their photographs show it to be rugged, perhaps because of imperfect preservation, but possibly suggestive of somewhat coarse sculpture. Now in *D. sulcata* from the Redoak Hollow the surface is coarsely pitted, the circular pits being somewhat distantly spaced one from another, especially toward the margins of the valve, where the pits almost disappear. The space of surface between the pits is quite smooth.

The distinctly transversely corrugated flange encircles the valve. It narrows gradually on way towards the dorsal edge, is narrower still after turning along this edge, and wedges out completely before reaching the dorsal flare of the sulcus. The narrowness of the flange is typical for the right valve of the genus *Deloia*, whose left valve has a more conspicuous and more corrugated flange.

No species of *Deloia* are known from the Pennsylvanian.

Family GLYPTOPLEURIDAE Girty, 1910
Genus GLYPTOPLEURA Girty
GLYPTOPLEURA COOPERI, n. sp.
Text-figs. 29,30; Pl. 4, figs. 19,20

1947. *Glyptopleura similis*, COOPER, Jour. Paleontology, v. 21, p. 90, pl. 22, figs. 32–34.

not 1939. *Glyptopleura similis*, CRONEIS & FUNKHOUSER, Denison Univ. Sci. Lab. Bull., v. 33, p. 352, pl. 10, fig. 4.
not 1941. *Glyptopleura similis*, COOPER, Ill. Geol. Survey, Rept. Inv. no. 77, pl. 7, figs. 23,24.

Representatives of genus *Glyptopleura* are very scarce in the lower Pennsylvanian of Southern Oklahoma and adjacent area. Bradfield (1935) describes only one species *G. whitei*, which he found in the lower Dornick Hills (Otterville limestone and somewhat below northeast of Ardmore). The best preserved specimen in the present collection is very close in shape, size, and ornamentation to the species from the Kinkaid limestone of Illinois illustrated by Cooper (1947, pl. 22, figs. 32–34), who identifies it with *G. similis* Croneis & Funkhouser (1939, p. 352, pl. 10, fig. 4), previously found only in Clore limestone. However, though the pattern of *G. similis* and the form which is here described as *G. cooperi* n. sp., have much in common, it seems that some differences between them, which Cooper might have thought to be mere variation within specific rank, appear more constant, as they are found in both the specimens from the Kinkaid of Illinois and in that from the Redoak Hollow of southern Oklahoma. Most obvious difference is in the length of the rib located anteriorly to the pit: it is extremely short in *G. cooperi*, while in *G. similis* the corresponding rib is not much different from the other ribs of the carapace. Furthermore the pit in *G. similis* is not located in the line with this rib, but above the next rib upward (dorsad). Furthermore, there are more short ribs in postero-dorsal part of the carapace in *G. similis* than in *G. cooperi*, and there are also various minor differences in the details of the pattern of the other ribs in the two species. Another late Chester (Clore to Kinkaid) species with which *G. cooperi* may be confused is *G. alternata* Croneis and Funkhouser (1939), but the latter has two pits, one above the other, the higher of the two apparently corresponding to a very slight interruption of the rib in *G. cooperi*. Also, the rib located anteriorly on the line of the lower pit is much longer in *G. alternata* than in *G. cooperi*. Otherwise these two species have more nearly the same sculptural pattern than the one in *G. similis*.

GLYPTOPLEURA WARTHINI, n. sp.
Text-figs. 27,28

This form is strangely reminiscent of *Glyptopleura perbella* Geis, which was established on the material from the Salem limestone of Indiana, that is stratigraphically far below the horizon of the Redoak Hollow. Similar are the oblong-rhomboidal outline of the carapace and the pattern of the sculpture; in these respects *Glyptopleura warthini* is closer to *G. perbella* than to any of the known species of *Glyptopleura* from the Chester. However, *G. warthini* is smaller, being .85 mm. long, while *G. perbella* averages 1.09 mm. in length; and the pattern of the sculpture most reminiscent of *G. perbella* is developed in what is believed to be instar (Text-fig. 5), and not so much in the adult of *G. warthini*.

GLYPTOPLEURA GEISI, n. sp.
Text-fig. 32; Pl. 4; figs. 22,23

The single left valve of this small species has been at first considered to be an instar of *Glyptopleura warthini*, n. sp., but when comparison was made with the species of this genus described by Geis (1932) from the Salem limestone of Indiana its similarity to *G. elegantis* Geis became evident. This similarity concerns not only the sculptural pattern of the valves, but also the outline of the dorsal edge: straight and angular anteriorly and posteriorly. In this latter respect *G. warthini* is quite different, its dorso-anterior and dorso-posterior edges being broadly rounded instead of angular.

The two new species of *Glyptopleura* from the Redoak Hollow, *G. warthini* and *G. geisi*, display the same peculiar relationship between themselves as that between *G. perbella* and *G. elegantis* from the Salem. In both pairs of species the forms mentioned in the first place are larger and have both dorsal ends rounded, while the forms mentioned in the second place are smaller in about the same proportion and have dorsal ends angular. The species from the Redoak Hollow are smaller than the corresponding species from the Salem; also, the larger of the two Redoak Hollow forms, *Glyptopleura warthini*, is a shade smaller than the small *G. elegantis* in the pair of species from the

Salem, see table 4. Should it be eventually concluded that the smaller carapaces of each of these stratigraphic pairs are instars of the larger ones, then the angular outline of the dorsal edges in their instars may be considered of phyletic significance in accord with the law of recapitulation. Adults of *Glyptopleura* that have such outlines are common in Renault formation of the Chester (*G. bristoli*, *G. hendricksi*, *G. elliptica*) and in the Salem (*G. karli*), and in the lower Chester belong also the species of related genus *Glyptopleuroides* (*G. girtyi*, *G. perplexa*, *G. insculptus*), whose postero-dorsal ends are also angular. Besides, the carapace of *Glyptopleuroides* and of the just mentioned early Chester and Salem species of *Glyptopleura* have oblong-rhomboidal outline. On the other hand all species of *Glyptopleura* in the higher Chester and the Pennsylvanian have the dorsal ends well rounded, and the whole outline of their carapace is subelliptical.

GLYPTOPLEURA SCOTTI, n. sp.
Text-fig. 31

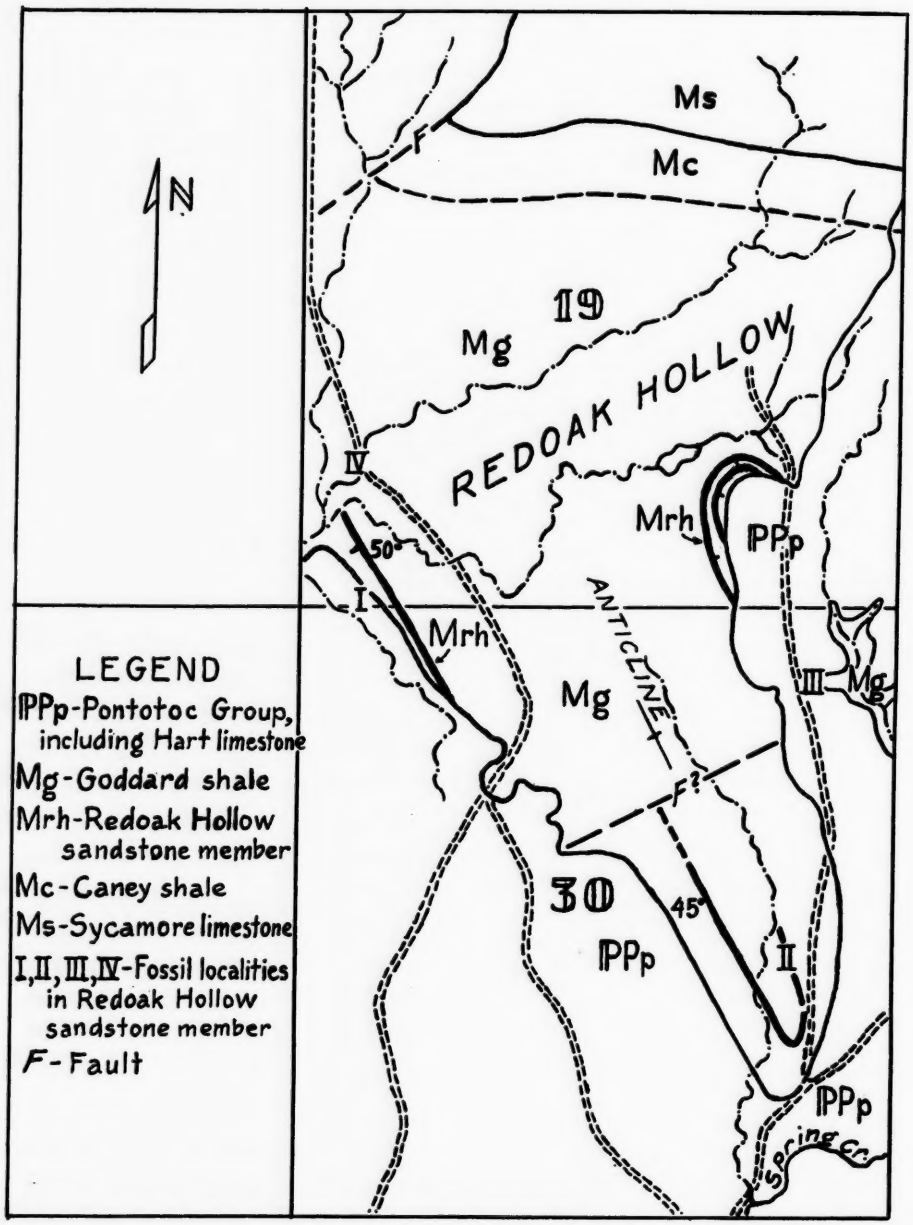
Most characteristic of this species is its nearly perfect elliptical outline, with probable flattening only of the dorsal edge which is imperfectly preserved. Both in the outline and the sculpture pattern it seems nearer to *Glyptopleura cooperi*, n. sp., more than to any of the previously described American Mississippian and Pennsylvanian forms. It differs from *G. cooperi*, however, in more perfect elliptical outline and its proportionally greater elongation, and also in details of sculpture. It has one less rib in both antero-dorsal quarter and in ventral portion, and all ribs have more or less distinct sag in the antero-dorsal quarter.

Among the previously described Mississippian species of *Glyptopleura*, *G. intermedia* Croneis & Gutke (1939) from the Golconda (but not that from the Glen Dean illustrated by Cooper, 1941, pl. 7, fig. 41) of the Chester is similar to it in approaching elliptical outline, but is proportionally less elongate and has different sculpture; and among the known Pennsylvanian species *G. menardensis* (Harlton, 1929) of the Upper Pennsylvanian of Texas has the same degree of similarity to *G. scotti* in the outline of the carapace as *G. intermedia*, and also differs in sculpture.

The single recovered inner mold of right valve is about .70 mm. long and .40 mm. high.

Family HOLLINIDAE Schwartz, 1926
Genus HOLLINELLA Coryell
HOLLINELLA RADIATA var. DOTTI, n. var.
Pl. 4, figs. 1–4

This is the largest and the most common ostracode in the Redoak Hollow. It has the typical features of the well known, trivial Lower Carboniferous (Mississippian) *Hollinella radiata* Jones & Kirkby: large size (1.4 mm. long); wide, flaring frill, attached nearly all around the valve, with the exception of the fringe line and the dorso-posterior quarter; a very large anterior node, its upper surface even with the hinge line; a much smaller posterior node, whose lower edge is only slightly below the lower edge of the anterior node; and the coarsely tuberculate surface, with scattered larger tubercles. It would be difficult to distinguish the form from the Redoak Hollow from the somewhat variable *H. radiata* of the Chester, if it were not for the extraordinarily high elevation of its anterior node above the surface of the shell, a feature called to my attention by Betty Kellett, when I consulted her on the Redoak Hollow ostracods. It seems that the elevation or height of this node above the surface of valve has not been usually measured, and the shell was seldom illustrated in such manner as to render possible to measure the height of the node on its photographs or sketches. Ulrich's sketch of *H. radiata* var. *cestriensis* (1891, pl. 14, fig. 4b) is an exception, and the height of the nodes measured on it is only circa .1 mm. The height of same in var. *dotti* is .25–.30 mm. In addition to the great prominence of the anterior node perhaps the following characters may prove of additional help in recognition of var. *dotti:* scarcity of larger punctae (like in the "spineless" example from the Clore illustrated by Cooper, 1941, v. 9, fig. 44), and not always developed or preserved small vertical cusp at the posterior end of the straight hinge line. One of the most completely preserved specimens (right valve) measures 1.4 mm. long and



TEXT-FIG. *45*—Geologic map of secs. 19 and 30, T. 2 S., R. 1 W., Carter County, Oklahoma, by C. W. Tomlinson, showing localities at which fossils were found in the Redoak Hollow sandstone member of the Goddard shale. NOTE: The stratigraphic unit called Redoak Hollow member of Goddard shale in Tomlinson's foreword and location map is called Redoak Hollow formation in the title and the paleontological text. The unit is mappable within about one square mile in the type area north of Milo, but has not yet been definitely identified on the surface elsewhere in the Ardmore basin.

.85 mm. high, the latter including .2 mm. wide frill.

H. radiata has not been found by Bradfield (1935) in the Dornick Hills or other Pennsylvanian formations of the Ardmore Basin, though he found in the same basin several species of genus *Hollinella* in the Deese and the Hoxbar. Harlton likewise did not find *Hollinella* in the Johns Valley formation nor in the Wapanucka. Among the previously known lower Pennsylvanian species *Healdia kellettae* Knight of the upper Des Moines seems the nearest to *H. radiata* and probably evolved from it. This upper Des Moines form is smaller (a little over 1 mm. long), more coarsely tuberculate and has more nearly sub-equal anterior and posterior nodes.

In comparison with the few published illustrations of *Hollinella radiata* from England the new variety differs in having the two nodes set at closer distance to each other, and undoubted absence of a spine at the posterior edge of the frill.

Family KIRKBYIDAE Ulrich & Bassler, 1906
Genus KIRKBYA Jones
KIRKBYA sp. cf. K. BENDENSIS Harlton
Pl. 4, fig. 18

1933. *Kirkbya bendensis.* HARLTON, Jour. Paleontology, v. 7, p. 22, pl. 6, fig. 2. Johns Valley shale and Wapanucka limestone, Oklahoma.
1935. *Kirkbya bendensis.* BRADFIELD, Bull. Am. Paleontology, v. 22, p. 50, pl. 3, fig. 5. Upper Morrow, southern Oklahoma.
1946. *Kirkbya bendensis.* COOPER, Ill. State Geol. Survey Bull. 70, p. 104, pl. 16, figs. 27–30. Fulda to Seville (upper Morrow and Atoka), Illinois.

The single specimen is an internal mold of a practically complete, though somewhat crushed left valve. It matches well the specifications of Harlton's species, though not without some discrepancies, which may be sufficiently important for its recognition as new variety of *K. bendensis.* It is like *K. bendensis* in its general outline and dimensions, with practically straight hinge line, the anterior edge meeting the hinge sharply, at an angle slightly less than 90°, the posterior edge somewhat rounded and meeting the hinge at a larger than 90° angle. It differs from *K. bendensis* by the position of sub-central pit, which is slightly below the center in *K. bendensis* and slightly above the center in the form from the Redoak Hollow. This difference may be considered merely individual variation, if the concept of the species is broadly understood. On the other hand, it may yet prove of stratigraphic importance, and therefore is here registered.

The previously described and illustrated examples of the species differ from each other in size, shape, position of central scar, and magnitude of reticulations of the sculpture (see table 4). The type from the Wapanucka limestone illustrated by Harlton is twice as long as high, with central scar only slightly below the center, and reticulations coarser than in any other examples illustrated. The example from the shale slightly below the Otterville (Upper Morrow) of Ardmore described by Bradfield has a length more than twice the height, with the central scar closer to ventral than to dorsal edge in a proportion about 2 to 3, and a finer reticulation of the sculpture. Cooper illustrates two examples of the species, a smaller example from the Fulda (correlated with the lower Wapanucka of Oklahoma), and a larger specimen from the Seville (correlated with the upper Atoka of Oklahoma). The smaller Fulda example is less than twice as long as high, has a very low central scar, and a pronounced shoulder behind the anterior edge, that rises above the hinge line—a feature not present in any other illustrated examples of the species. The larger Seville example has normal dimensions, twice as long as high, a position of scar like in the example illustrated by Bradfield, and has about as many reticulations per given space, as the latter. The reticulations in the new example from the Redoak Hollow match the same in the examples from the Seville of Illinois and from the upper Morrow of the Ardmore Basin, Oklahoma.

Among the described species of *Kirkbya* from the Chester of Illinois only *K. elongata* Cooper (1941, p. 46, pl. 10, fig. 50) approaches *K. bendensis* in general outline, but unfortunately the sculpture of its single individual is not preserved and neither is the central scar. The length is more than twice the height, about the same proportion as in

the example of *K. bendensis* from the Upper Morrow at Ardmore and in the new example from the Redoak Hollow. *K. elongata* is rare in the Paint Creek formation, that is lower Chester (New Design Group). Among the known species of *Kirkbya* from the Kinkaid of Illinois *K. intermedia* Croneis and Thurman is twice as long as high, just as *K. bendensis*, but differs in having obtuse dorsal (cardinal) angles anteriorly and posteriorly. In the other similar species, *K. symmetrica*, from the Kinkaid, these two angles are sharper, about 90° each, unlike the unequal angles in *K. bendensis*.

KIRKBYA SYMMETRICA Croneis & Thurman
Pl. 4, fig. 5

1938. *Kirkbya symmetrica*. CRONEIS & THURMAN. New ostracodes from the Kinkaid formation: Denison Univ. Sci. Lab. Bull. v. 33, p. 310–311, pl. 7, figs. 4–6.
1941. *Kirkbya symmetrica*. COOPER. Chester ostracodes of Illinois: Ill. Geol. Survey Rept. Inv. no. 77, p. 18, pl. 10, figs. 31–33.

A single external mold of a valve, damaged by some apparently pre-burial cracks and distortions, seems identical with *K. symmetrica* from the Kinkaid in shape, size, sculpture, and ventrad position of pit.

Cooper records *K. symmetrica* in the Kinkaid and the Menard formations (1941, p. 18), but illustrates a specimen only from the Kinkaid.

Genus AMPHISSITES Girty
AMPHISSITES BRADFIELDI, n. sp.
Text-figs. 9–11; Pl. 4, figs. 8–17

The new species is established on external molds of two adults, which are dorsally incomplete, and two complete instars, all of right valves. It resembles *Amphissites marginifera* Roth from the Wapanucka on one hand, and some upper Chester forms on the other, particularly *A. weaveri* from the Fayetteville and *A. insignis* from the Kinkaid. Similarly to all these forms it has one marginal keel that runs all around the carapace except along dorsal margin, and two false keels that run generally parallel to the marginal keel. The lowest, submarginal false keel is separated from the marginal keel by three rows of reticulations in the middle part of the venter and to the antero-ventral angle, but from this angle and up (toward dorsum) the distance between these keels increases to four rows of reticulations along the posterior part of the venter, but from the ventro-posterior angle and up it tends to narrow down. The complete instars show confluence of marginal and submarginal keels toward dorsal edge, the keels being fused at sharp angles slightly below the dorsum on either side of the carapace, but at a lower point at the posterior than at the anterior. The second false keel runs parallel to the first ventrally, with the distance of three rows of reticulations between them, and the same distance separates them along the anterior, with only a very slight widening toward the dorsum and with a final addition of a fourth row of reticulation when near to the antero-dorsal angle. At postero-ventral angle the second false keel makes an upward turn with a resulting sudden widening of the distance between it and the first keel to five, and a little higher up to six rows of reticulations. The third false keel consists of an anterior and a posterior short links, that start at obtuse angles from the anterior and the posterior parts of the second false keel, and tend to meet in the center of the central elevation, but peter out as soon as they swing upwards, in an attempt to climb over it. In the development of the third false keel *Amphissites bradfieldi* resembles closely *A. insignis* of the Kinkaid, and particularly the specimen illustrated by Cooper (1941, pl. 9, fig. 32), and resembles less the original illustrated by Croneis & Thurman (1939, pl. 8, fig. 13). The specimen illustrated by Cooper is smaller than the original and its third false keel also fades out toward the center of the central elevation, while in the original specimen, which, if same species, is an adult, the third false keel runs over central elevation without losing its strength. Besides, rudiments of a fourth false keel can be seen above the third keel, a feature absent in the smaller individual illustrated by Cooper. Thus, the new species from the Redoak Hollow is more like instar than adult of *A. insignis*. It differs from *A. insignis* only by smaller size, adult being .9 mm. long, and perhaps by the slight central concavity of the ventral edge, which in *A. insignis* is very gently convex to straight (in the middle). The central position and size of central elevation, and the longitudinally

elongated scar below the postero-ventral angle of the central elevation are identical in the two species.

Genus POLYTYLITES Cooper, 1941
POLYTYLITES ? KELLETTAE, n. sp.
Text-fig. 34

The single left valve is questionably referred to genus *Polytylites* because only its internal surface is exposed, which prevents observation of possible presence of carinae near free margin, one of the generic characters of *Polytylites*, as per its diagnosis by the originator of the genus, C. L. Cooper. On the other hand, other features of the genus are said to be as follows: "Kirkbyidae with small to large, circular to ovate central node, with low to prominent, short to elongate shoulders or swellings in dorsal extremities" and a "surface marked by kirkbyan pit below central node and fine to coarse reticulations" (Cooper, 1941, p. 51).

All these characters are present in the described new species, except that only posterior shoulder is clearly developed, while anterior shoulder is insignificant. However, similar situation with "poorly developed" anterior shoulder has been already noted by Cooper for his *Polytylites diversus* from the Vienna limestone of Illinois. *P. kellettae* is certainly near to it not only in this, but in other respects, as follows: *P. kellettae* is very small, about .45 mm. long, with greatest height near posterior edge; the central node is not prominent, and slightly closer to the posterior than to the anterior; the pit is below the center of the shell and at the lower posterior end of the central node. Reticulation of the surface of the carapace has about the same pattern as in *P. diversus* but is distinctly finer. Judging by the very thin depression, which is parallel to the free (ventral) edge and is separated from it by two parallel rows of ornamental pits, there is only one carina in the valve, just as is the case in *P. diversus*.

There seems to be only one clearly recognizable difference between *P. diversus* and *P. kellettae:* the latter has a finer sculpture, that is its reticulations are smaller, so that more of them can be counted per the same space; thus counting the rows of reticulate sculpture on the photograph of the left valve of *P. diversus* (Cooper, 1941, pl. 10, fig. 4) there are 17 rows from the anterior to the posterior edges, while on the left valve of *P. kellettae*, which has the same size, there are 23 rows of reticulations.

POLYTYLITES CORYELLI, n. sp.
Text-fig. 33

Although only one internal mold (of right valve) is recovered, in which only a slight linear elevation along the ventral edge suggests possible presence of carina, the form is referred to genus *Polytylites* because of close resemblance of its shape and sculpture to *Polytylites wilsoni* (Croneis & Gutke, 1939, p. 47–48, pl. 2, figs. 24,25; Cooper, 1941, p. 54, pl. 11, figs. 22,23). *P. coryelli* differs from the latter only in smaller size, and a greater downward extension of the anterior node. The new species is close in size to the smallest recorded specimens of *P. bradfieldi* (Croneis, 1939, p. 29; Croneis & Funkhouser, 1938, p. 346–347, pl. 10, fig. 15, originally described as *P. rothi* C. & F., not *P. rothi* Bradfield, 1935); but in regard of the sculpture the latter is even more different from the new species than *P. wilsoni*, particularly in the shape of the middle node, which is round in *P. bradfieldi*.

The single individual of *P. coryelli* is .56 mm. long and .26 mm. high. Its anterior node is wider than the middle node, but the latter is more sharply differentiated, particularly in its ventral side. These two nodes are nearly equally long, and both are appreciably forwardly inclined. The dorso-anterior edge is slightly concave, and so is also the ventral edge. The posterior node is a mere small elevation at the dorsal edge. The surface of the internal mold shows faint reticulation, the external side of the carapace being apparently more strongly reticulate.

POLYTYLITES LEVINSONI, n. sp.
Text-figs. 25,26; Pl. 4, figs. 6,7

Outer and inner molds of one right valve recovered. Carapace trinoded, with anterior shoulder (node) projecting above hinge. Reticulation of the surface not extending over anterior half of central node, whose top reaches hinge and whose smooth surface is sharply delineated posteriorly by a straight

sub-vertical border line. Kirkbyan pit obscure. Single carina parallels free margins.

Length .65 mm.; height .34 mm.

Size and extension of the central node to hinge are similar to the lower Chester forms *P. ambitus* and *P. wilsoni* (Cooper, 1941), but *P. levinsoni* is smaller and unlike these and other species of *Polytylites* in having half of central node smoothly surfaced.

Genus ROUNDYELLA Bradfield
ROUNDYELLA BELLATULA Bradfield
Text-fig. 12

1935. *Roundyella bellatula*, BRADFIELD, Bull. Am. Paleontology, v. 22, no. 73, p. 66–67, pl. 4, fig. 11.

Outer mold of a single, ventrally incomplete valve recovered. Elongately oval shape of carapace 1 mm. long and about half as high as long, with sub-central pit and reticulate surface are all similar to *R. bellata*, hence allowing its identification in spite of broken ventral edge.

Original of the species comes from just below Otterville limestone (Morrow Series) of the Ardmore basin, and the present identification lowers the range of *R. bellatula* to the Redoak Hollow of the same basin.

Family BAIRDIIDAE Sars, 1888
Genus BAIRDIA M'Coy
BAIRDIA BILLJOHNSONI, n. sp.
Text-figs. 40,41

Two right valves of the same species have been found on the same fragment of rock; one is internal mold and the other consists of slightly more than a half of valve, which partially covers a nearly complete internal mold—the second specimen is selected as the holotype.

The species is named after William R. Johnson, formerly paleontologist of the Nebraska Geological Survey.

The most characteristic of the species is its greatly elongated shape, and a sharply and gradually terminated anterior end and, particularly so, the sharp posterior end. Its elongately-acute shape resembles that of *Bairdia renaultensis* (Croneis & Gutke, 1939, p. 59–60, pl. 1, figs. 5,6; Cooper, 1941, pl. 2, figs. 9,10), but the latter has concave ventral edge, and much larger angle of posterodorsal slope (about 40–45°, judging by the photographs). *Bairdia osorioi* (Cooper, 1941, pl. 2, figs. 13,14)[1] is still nearer to *B. billjohnsoni* in shape, but it has also a slightly concave ventral edge and less acute posterior end. *Bairdia aculcata* from the Kinkaid (Cooper, 1941, p. 24, pl. 1, figs. 47,48) has a posterior terminated about as sharp as in *B. billjohnsoni*, but posterodorsal slope is larger (30–35°) than that in the latter, and the carapace is much higher relative to length. Closer than all mentioned species to *B. billjohnsoni* is *B. biacuta* from the Lower Dornick Hills of the Ardmore Basin (Bradfield, 1935, p. 19; 78–80; pl. 5, figs. 5a,b), but *B. billjohnsoni* is still narrower and has still sharper posterior end: judging by the sketch in Bradfield's paper the angle of posterodorsal slope in *B. biacuta* is about 30°. Bradfield's illustrated specimen is referred to the Lester limestone, and the same is mentioned as the occurrence of the species in the text. However, in the Faunal Chart of stratigraphic distribution of the forms (1935, p. 19) the species is indicated to be common in the Pumpkin Creek (apparently an error, and should be the Lester), and an occurrence of poorly preserved species is also indicated in the interval between the Otterville and the Jolliff. It seems likely that the latter will prove identical with the new species *B. billjohnsoni* from the Redoak Hollow rather than with *B. biacuta*.

The dimensions of the two individuals of the new species are 1.1 mm. and .9 mm. long, and .36 mm. and .30 mm. high, the larger figures are those of the holotype. The angle of the posterodorsal slope about 20°, which is perhaps the smallest on record for any species of *Bairdia*. The surface of carapace is punctate, the punctae being gently reflected also through the thin carapace on the surface of its internal mold. A distinct but narrow and flattened border runs along the whole ventral edge and broadens at the extremities, but ends quickly as soon as it climbs over to the dorsal edge. Very sharp posterior end is located in the middle between the dorsal and ventral edges, and the slopes on either side of it are of same inclina-

[1] Cooper credits the naming of this species from the Golconda to Croneis & Gale, but in their paper on the New Ostracoda from the Golconda formation (the only joint paper published by them), there is no description or illustration of a species thus named, or any other *Bairdia* like it.

tion (total angle about 40°). Anterior end is elevated to a position ¼ to ⅓ of the total height below dorsal edge, and nearly straight anterodorsal slope meets sharply at about 70°–80° with the gently and evenly rounded anteroventral slope.

BAIRDIA CRONEISI, n. sp.
Text-fig. 42

This is one of the smallest and about the narrowest species of the genus, and could be considered an immature instar of *Bairdia billjohnsoni* just described, if it were not for its sharper anterior end, the subequal postero-dorsal and antero-dorsal slopes, and the centralized position of the posterior and anterior ends. It is reminescent of *Bairdia symmetrica* from the Trivoli zone (basal Missouri Series) of Illinois (Cooper, 1946, p. 52, pl. 3, figs. 37,38), but the latter species is proportionally much higher, and is of larger size (1 mm. long). Besides, *Bairdia croneisi* has dorsal edge flattened in the middle. Its length is about .8 mm. and height .23 mm. In these dimensions and elongated shape it is even more nearly like *Bairdia biacuta* Bradfield (1935, p. 79–80, pl. 5, figs. 5a,b) from the Lester limestone at Ardmore, which is .76 mm. long and .3 mm. high. However, *Bairdia croneisi* differs from it in more nearly centralized position of both sharp ends, and in flattened dorsal edge.

BAIRDIA MULTIHILOSA, n. sp.
Text-fig. 43; Pl. 4, fig. 18

?1947. *Bairdia attenuata* COOPER (not GIRTY, 1910, p. 237), Jour. Paleontology, v. 21, p. 84, pl. 21, figs. 27,28.

Two external molds of left valve have been uncovered. Valve has subtriangular shape, with highly arched dorsal margin, and its surface bears a multitude of characteristic small subcircular pits, a kind of sculpture previously observed on very few species of *Bairdia*, whose surface is usually smooth to granulose. It appears that pitted or punctate surface has been previously noticed in three American species only: *B. aequa* Cooper (1941, p. 24–25, pl. 1, figs. 21,22) from the Renault formation of Chester group, whose surface "appears finely pitted"; *B. menardensis* Harlton from the Des Moines and higher Pennsylvanian, whose surface is said to be "finely granulose to punctate" (Cooper, 1946, p. 47); and *B. punctata* Bradfield (1935, p. 79, pl. 5, figs. 7a,b) from the Deese group (=Des Moines series) at Ardmore, whose carapace is described as "punctate." All three mentioned forms and *B. multihilosa*, n. sp., have in common not only the pitted character of the surface, but also highly arched dorsal margin, while the ventral margin is more or less flattened in the middle. *B. multihilosa* differs from both Mississippian and Pennsylvanian pitted forms by proportionally more elongated caparace, which is .85 mm. long and .40 mm. high, or more than twice as long as high. All previously described pitted forms are less than twice as long as high. In size the Mississippian *B. aequa* is about equal to *B. multihilosa*. while the two Pennsylvanian forms are much larger (1.32 and 1.39 mm. long). If the forms belong to a single phyletic branch the evolutionary trend toward larger size is thus clearly indicated.

Cooper identified twice the species of *Bairdia* which Girty described (but not illustrated) under the name *B. attenuata* (1910, p. 237) from the Fayetteville shale of Arkansas. The first form identified with *B. attenuata* by Cooper is referred to the Paint Creek-Golconda and illustrated on Pl. 1, figs. 17–20 (Cooper, 1941) as a smooth surfaced carapace. In this respect it is indeed like the original from the Fayetteville, whose carapace according to Girty's description has "surface smooth" (1910, p. 237). However, the second form referred by Cooper to *B. attenuata* comes from the much higher stratigraphic position, the upper layers of the Kinkaid of Illinois, and the photograph (Cooper, 1947, pl. 21, fig. 28) of this carapace shows distinctly pitted surface. Because this latter form seems identical with *Bairdia multihilosa*, n. sp., in shape, size, and apparent pitting of the carapace, and occupies about the same stratigraphic position, it is placed here provisionally in the synonymy of this new species from the Red-oak Hollow.

Family HEALDIIDAE Harlton, 1933
Genus HEALDIA Roundy
HEALDIA HARLTONI, n. sp.
Text-fig. 14

This small form is fairly common at localities No. 1 and No. 4. It is only about .4 mm.

long and slightly more than .2 mm. high. Its dorsal margin is angular, the apex being slightly closer to the anterior than the posterior. Ventral edge is nearly straight, with insignificant concavity in the middle. The anterior is rounded broader than the posterior, but the latter is more inflated and bears a very faint straight transverse ridge, whose ventral end is slightly closer to the posterior than dorsal end. Each end of the ridge tends to be produced into an insignificant node. Posterior slope of the dorsal bears slight depression. There is a faint transverse depression in both valves below the angularity of the dorsal, a feature generally not common in genus *Healdia.*

The species may be easily confused with *Healdia caneyensis* Harlton, which has been repeatedly described, especially if the species is understood in broad sense. In this case, however, its stratigraphic usefulness seems to be seriously impaired. However, in the original and all subsequent descriptions and illustrations of *H. caneyensis* by Harlton (1927, 1929, and 1933) and also by Bradfield (1935), the species is characterized, among other features, by a wider and thicker posterior, where a ridge is developed, and by a narrower and thinner anterior. In contrast with this the new species *H. harltoni* has its anterior wider than the posterior. Besides, it is only half the average size of *H. caneyensis*, the latter measuring .9 to 1 mm. long. It appears that the form from the Glen Dean (middle Chester) of Illinois, classified by Cooper (1941, p. 30) as *H. caneyensis*, belong rather to *H. harltoni.* Its anterior and posterior are of about equal width, its length (.57 mm.) intermediate between *H. harltoni* and *H. caneyensis*, and its ridge thicker than in either of the two and is conspicuously convex posteriorly. Thus it seems that *H. caneyensis* is an exclusive Morrow form, and a descendent of *H. harltoni.* Of course, if the three discussed species belong together phylogenetically, transitional forms between them may be expected.

OSTRACODES ILLUSTRATED BY SKETCHES BUT NOT DESCRIBED

Following is a list of molds whose imperfect preservation makes their identification quite hazardous. Their sketches are appended so as to point out the presence in the Redoak Hollow of a greater number of ostracode species than as identified and described with a varied degree of accuracy:

Cavellina (?) sp., Text-figs. 21–23; ×30.

Johnesina (?) sp., Text-fig. 15; ×100.

Hollinella sp. cf. *H. oklahomensis* Harlton, Text-fig. 20; ×40.

Paraparchites (?) sp., Text-fig. 19; ×40.

Internal valve of an ostracode, Text-fig. 24, ×40.

DISCUSSION OF OSTRACODES

When describing the stratigraphically latest Mississippian fauna from the Kinkaid of Illinois, Cooper states (1947, p. 85) that:

> ". . . the fauna described is from the youngest Mississippian beds in the type area, which can be studied in connection with the Mississippian-Pennsylvanian contact. While predominantly Chester, the micro fauna reflects other Chester faunal and sedimentological characteristics in that it heralds the approaching Pennsylvanian by showing a distinct break from the Middle Mississippian, while at the same time containing some early Pennsylvanian elements. All of the fauna, with the exception of the foraminifer *Trepeilopsis* and the ostracode *Hollinella radiata* show a complete lack of Middle or Lower Mississippian affinity, while most of the Foraminifera, including the fusuline *Millerella*, and some ostracodes and conodonts have a distinctly Pennsylvanian character."

Croneis & Thurman (1938, p. 300) previously pointed out that the Kinkaid ostracodes, "are markedly similar to some Pennsylvanian forms. Particularly is this true of species of *Amphissites* and *Kirkbya.*" The present analysis and discussion of the ostracodes from the Redoak Hollow and the related forms indicate that the two genera of the ostracodes from the Kinkaid particularly mentioned by Croneis & Thurman are indeed very close to the subsequently developed and common Pennsylvanian forms.

Most instructive is the presence in the Redoak Hollow of the late Mississippian ostracode *Polytylites*, which can be considered subgenus of *Amphissites*, and whose representatives have not yet been recognized above the Mississippian; and this is also the case with the genera *Carboprimitia* and *Deloia.* The fairly common occurrence of genus *Glyptopleura* in the Redoak Hollow is also an indication of its late Mississippian

age, while in late Morrow time the representatives of *Glyptopleura* became suddenly very rare; they are represented by a single species in the Upper Morrow of the Ardmore Basin, and this form does not resemble closely any of the common Redoak Hollow and other late Mississippian forms.

Other well differentiated species of various genera, such as *Bairdia multihillosa*, n. sp., and *Sansabella truncata* Cooper are distinctly late Mississippian forms, and are succeeded by different representatives of the same genera in the same area in late Morrow time.

On the other hand, there is in the Redoak Hollow a conspicuous change in *Hollinella radiata*, as this species suddenly mutates into a form with a much higher anterior node, a feature typical for the closely related common Pennsylvanian species of the genus.

When the total number of the ostracodes in the Redoak Hollow which show their closest relationship to forms preceding or succeeding them in the geological time is compared, the Mississippian relationships seem to be outweighting the Pennsylvanian ones in a ratio of nearly 2 to 1 in favor of the earlier time, see table 5 illustrating this conclusion.

Evidence of presence of additional genera and species of ostracodes in the Redoak Hollow is at hand in form of partly too fragmentary and partly too indistinctly preserved molds, which are too difficult to classify. These undescribed remains indicate the presence of *Beyrichia*, *Sulcella*, and possibly other genera. It is not possible at the present to hazard an opinion whether the local species of these genera are likely to indicate stronger affinity toward the Mississippian or Pennsylvanian forms.

THORACICA

Genus TURRILEPAS Woodward

1865. *Turrilepas*, WOODWARD, Quart. Jour. Geol. Soc. London, v. 21, p. 486–489.
pars 1888. *Turrilepas*, CLARKE, *in* HALL & CLARKE, N. Y. Geol. Survey, Paleontology, v. 7, p. lxiii.
1918. *Turrilepas*, CLARKE, *in* ZITTEL, Text-Book of Paleontology 2nd Am. ed., p. 744 (1896, 1st ed., p. 649).

Woodward (1865) introduced generic name *Turrilepas* for the Silurian (Wenlock) fossil originally placed by de Koninck (1851, p. 199) in the living genus *Chiton*. However, Woodward reasonably proved it to be rather a cirriped, an interpretation now generally accepted.

Clarke discovered scattered plates of genus *Turrilepas* in the Hamilton (highest Middle Devonian) of New York, where this fossil is accompanied by another genus of cirripeds named by Clarke *Strobilepis;* see its description below. Isolated plates of *Turrilepas* and related new genus *Clarkeolepis* are encountered in the Redoak Hollow; they

TABLE 5—COMPARISON OF THE OSTRACODS FROM THE REDOAK HOLLOW FORMATION WITH THE FORMS STRATIGRAPHICALLY BELOW AND ABOVE THEM

Chester Series	Redoak Hollow formation	Morrow Series
Paraparchites ovatus Cooper	*Paraparchites* (?) cf. *elongatus* Bradfield	*P. elongatus* Bradford
Sansabella truncata Cooper	*Sansabella* cf. *truncata* Cooper	*S. amplectus* Roundy
	Sansabella keslingi, n. sp.	
Sargentina allani Coryell and Johnson	*Sargentina* cf. *allani* Coryell and Johnson	
Carboprimitia rotunda Croneis and Funkhouser	*Carboprimitia* cf. *rotunda* Croneis and Funkhouser	*Jonesina biformis* Bradford
Nuferella wellsi Coryell and Sohn	*Nuferella rothi*, n. sp.	*N. infrequens* Bradfield
Jonesina springera Cooper	*Jonesina* cf. *springera* Cooper	
Deloia sulcata Croneis and Funkhouser	*Deloia sulcata* Croneis and Funkhouser	
Glyptopleura symmetrica Croneis and Funkhouser	*Glyptopleura cooperi*, n. sp.	*G. coryelli* Harlton
Glyptopleura perbella Geis	*Glyptopleura warthini*, n. sp.	
Glyptopleura elegantis Geis	*Glyptopleura geisi*, n. sp.	
	Glyptopleura scolti, n. sp.	
Hollinella radiata (Jones and Kirkby)	*Hollinella radiata* var. *dotti*, n. var.	*H. gibbosa* Kellett
Kirkbya symmetrica Croneis & Thurman	*Kirkbya symmetrica* Croneis and Thurman	
	Kirkbya cf. *bendensis* Harlton	*K. bendensis* Harlton
Amphissites weaveri Roth	*Amphissites bradfieldi*, n. sp.	*A. illinoisensis*, n. sp.
Polytylites diversus Cooper	*Polytylites kellettae*, n. sp.	*P. wapanuckensis* (Harlton)
Polytylites wilsoni Croneis and Gutke	*Polytylites coryelli*, n. sp.	
	Polytylites levinsoni, n. sp.	
	Roundyella bellatula Bradfield	*R. bellatula* Bradfield
Bairdia aculcata Cooper	172. *Bairdia billjohnsoni*, n. sp.	
	173. *Bairdia croneisi*, n. sp.	*B. biacuta* Bradfield
Bairdia granireticulata Harlton	174. *Bairdia multihilosa*, n. sp.	*B. punctata* Bradfield?
Healdia cf. *caneyensis* Harlton	175. *Healdia harltoni*, n. sp.	*H. caneyensis* Harlton

Note: Solid lines indicate identity or close relationship of the species; dotted lines indicate their more distant relationships.

constitute the highest known stratigraphic occurrence of both. Previously the range of *Turrilepas* was indicated as "Cambrian (?) to Upper Devonian" (Clarke, 1918, p. 744).

TURRILEPAS WHITHERSI, n. sp.
Pl. 4, figs. 12,13

Three isolated plates of this species have been recovered, and the most complete one is designated as holotype. The practice of making species on the evidence of isolated plates alone was initiated by Clarke (1888), who realized its biological shortcomings because of considerable variation within the sets of plates that belong to a single capitulum of this fossil cirriped. However, in view of the fact that in by far the most cases only isolated plates of this genus are encountered, their taxonomy, in order to be stratigraphically useful, should be based on the isolated plates, as Clarke suggested. The plates of the new species *T. Whithersi* are about 1.3 mm. high and 1.5 mm. wide, sharply angled (at about 120°) along a straight line into two equal halves. Both halves are plane and smooth, covered only with narrow concentric elevations representing growth lines. The lines are spaced closer near the apex, but become nearly equidistantly spaced over the greater part of the plate. They are sinuous on the longer half and broadly convex on the shorter half. The longer half is .8 mm. broad, and the shorter .6 or .7 mm. broad. The species differs from all previously described Devonian and older species by having sharper angulation and smaller size. Woodward (1865) did not measure the individual plates of his species, and did not indicate the magnitude of the magnification of the enlarged sketches of its plates. However, judging by the natural size sketches of the assemblages, where the plates greatly overlap each other, the individual plates of *Turrilepas wrightii* (de Koninck), which he redescribed, are about 1 cm. or little less. Devonian species *Turrilepas tener* Clarke, which is the nearest to the new species from the Springer, is about 3.5 in height and width, as Clarke (1888, p. 219) measured it; while the plates of our species are about 2.5 mm. high. Furthermore, the angulation of the plates of *T. whithersi* is not accompanied by development of carina along its length, but only minute upward jog in the concentric lines of growth.

CLARKEOLEPIS, n. gen.

pars 1888. *Turrilepas*, CLARKE, *in* HALL & CLARKE, N. Y. Geol. Survey, Paleontology, v. 7, T. *cancellatus* only: p. 216, pl. 36, fig. 2.

Among all numerous plates which Clarke classified in *Turrilepas* and described under number of new specific names, one only, named *T. cancellatus*, is ornamented not only with concentric but also with radiating sculpture. However, Clarke did not attempt to modify generic diagnosis of *Turrilepas* so as to include plates with radiating costae, and mentions only that its plates "are covered with strong, somewhat elevated concentric lines" (Clarke, 1888, p. lxiii). On the other hand he notes that in his new related genus *Strobilepis* the calcareous and comparatively thick plates have their surface "ornamented by fine concentric wrinkles of growth, and *low radiating furrows and ridges*, and entirely covered with minute punctae" (*ibid.*, p. lxiii, my italics). Hence in view of these two diagnoses it seems that the above mentioned plate of *T. cancellatus* should be classified with *Strobilepis* rather than with *Turrilepas*. However, Clarke did not do so apparently because in the plates of the genotype of *Strobilepis* punctate character is constant, while presence of radiating furrows and ridges is not, and in the plate of *T. cancellatus* no punctae are present. Apparently Clarke was quite right in this decision, and the species does not belong to genus *Strobilepis;* but it seems that neither could it be referred to *Turrilepas*, and the present discovery of several plates of the same type in the Redoak Hollow provides an opportunity for introduction of a new generic name for their reception. Because only isolated plates of the new genus are known the following generic diagnosis concerns only the plates:

Plates small, plane or with sharp to broadly rounded angulation, which divides them into two uneven halves; ornamented with narrow more or less equidistantly spaced concentric elevations, which become fainter and more closely spaced at the basal edge of the plates; the spaces between the concentric elevations are

ornamented with densely spaced narrow radiating costae. The surface bears no punctae.

CLARKEOLEPIS CLARKEI, n. sp.
Pl. 4, figs. 14,15

The two plates for which this specific name is introduced are of nearly the same size and sculpture, but angulation in one is much sharper than in the other, while the position of sinuosity of the growth lines and of other details in the sculpture indicate that the two plates belong to the opposite (right and left) rows in the capitulum of this cirriped. The difference in sharpness of angulation seems well within variability of the various plates in a single capitulum of related genera as described and illustrated by Clarke (1888).

The plates are about 1.5 mm. wide and 2 mm. high. The plate with rounded (not sharp) angulation is selected as holotype. Its slightly incomplete height is 2 mm., and width 1½ mm. Its surface is marked by 7 narrow, equidistantly spaced concentric elevations (6 per 1 mm.) and two additional slightly less prominent elevations which are spaced somewhat closer and located at the base of the plate. There are also exceedingly faint concentric lines of growth between the concentric elevations. The surface between the concentric elevations is covered by very densely spaced radiating costae. The radiating costae and the concentric elevations both become gradually fainter toward the lateral edge of the shorter half of the angulated plate. In the longer half of the same, where the concentric elevations make a sinuous curve, the radiating costae are fainter in the middle part near the basal edge, but become stronger again in the part toward its lateral edge.

The second plate has also a slightly incomplete height of 2 mm. and 1½ mm. width. It has been accidentally broken along the angulation in the course of preparatory work, but nevertheless shows clearly a sharp angulation at a slightly obtuse angle not greatly exceeding 90°. However, the sculpture of this plate is much like that in the first plate, with 8 principal narrow concentric, equidistantly spaced elevations; two additional, less prominent and more densely spaced elevations are located near the basal edge; and a few even more densely spaced and very faint elevations are located at the very edge. The space between the concentric elevations is covered with radiating costae, sharply defined and densely spaced, much like those in the first plate. These costae become less distinct as they approach the basal edge of the plate, and also when they approach the lateral edge of the shorter half. In the preserved part of the longer half these costae become less distinct in a wedge-like middle area near the basal edge, much in the same manner as they do in the corresponding area of the first plate.

The plate of *Clarkeolepis cancellatus* from the Devonian of New York differs from the equally small plate of *C. clarkei* by being ornamented with fewer and, therefore, more distantly spaced radiating elevations: about 4 per 1 mm.

CLARKEOLEPIS ELEGANS, n. sp.
Pl. 4, fig. 16

Only one, not quite complete plate of this species has been recovered, and it is somewhat arbitrarily differentiated from the plates of *C. clarkei* by the absence of angulation and less equidistant spacing of the concentric elevations. It is possible that this plate belongs to the same species with the other two plates, representing the middle row of plates in a capitulum, but it is described under different specific name in following the taxonomic treatment initiated by Clarke, see the discussion under genus *Turrilepas*.

It seems that only about ⅔ of the whole plate is preserved, and the preserved part has a sharp, obtusely angular upper or dorsal edge, and sinusoid ventral edge. Its surface is ornamented by concentric wavy narrow elevations: fine elevations nearest to dorsal edge are distantly spaced (about 4 per 1 mm.), and additional four of fine fainter elevations are crowded at the ventral edge. All concentric elevations terminate abruptly at the dorsal edge; they are most prominent near this edge, and as they run away from it they become slightly less prominent, and almost fade out near the ragged line of break to the right. Very faint lines of growth can be observed between the concentric elevations in some parts of scale, particularly in

the right part, where the concentric elevations curve into most prominent lobe.

The spaces between the concentric elevations are covered everywhere with densely spaced radiating costae, which tend to be oriented perpendicular to the curvature of the concentric elevations.

PROBLEMATICA

CYCLOPUNCTA GIRTYI, n. gen., n. sp.
Pl. 3, figs. 14,16

1909. "Little round spots or punctae," GIRTY, U. S. Geol. Survey Bull. 377, p. 53–54, pl. 6, fig. 6.

Although the true nature of the enigmatic round punctae upon the shells of cephalopods can be only roughly hazarded, it seems desirable to classify them in order to call attention to their biological interest and apparent stratigraphic importance.

These punctae appear in considerable number, and, although generally irregularly scattered, seem to concentrate in certain fashion tending to follow, as it were, the lines of growth of a conch.

The size of these punctae is more or less uniform, but it varies slightly, from .1 to .3 in Girty's example, as measured on his illustration (Girty, 1909, pl. 6, fig. 6), which measurements correspond closely to the same range of variability (within a slight allowance for the errors of indicated magnification) in the present example from the Red-oak Hollow. Girty believes that these punctae "represent perforations in the shell" and adds that "no other conclusion seems possible from my observations," which are as follows:

> "In some cases the shell is replaced by transparent calcite and these prolongations of the matrix can be clearly seen traversing it. They thus pass nearly, if not quite, through the test. They appear partly as elevations and partly as depressions on the same specimens, according, I believe, as they break off near one or the other of the two surfaces of matrix to which they are attached. These perforations occur with equal abundance upon the small camerated frustums. They are, I believe, an intrinsic character of the shell and occur in other forms also. They are too equal in size, too regular in distribution, and too invariably transverse to have been produced by a boring animal."

(Girty, 1909, p. 53–54).

Thus, while Girty concludes that they could represent only "perforations," he ends with the belief that these could not be produced by a boring animal but are "intrinsic," that is belonging to the constitution or nature of the shell.

The fact that the very same kind of punctae are now discovered in the shell of *Cravenoceras*, a coiled ammonoid, while Girty found them on a straight shelled nautiloid, provisionally classified with *Boctrites*—eliminates the possibility of its intrinsic nature in the shell. Therefore, the alternative possibility, which he considered, that it represents "perforations" by a boring animal, should be reconsidered.

The present observation, coupled with what can be seen clearly on the fine enlarged reproduction of Girty's material, indicate that the punctae are shallow sub-hemispherical holes, not unlike circular depressions left by pellets of buckshot fired against hard board. Girty also observes that they "pass nearly, if not quite, through the test." Taking all this into account it seems permissible to conclude that the punctae are in reality mere depressions, not perforations in the shell of various unrelated cephalopods. Furthermore, their mode of occurrence suggests that they have been made by small, gregarious animals through their attachment in concentration upon these shells, and not necessarily by perforation.

It seems that the only living marine animal, that is known to attach itself in a number of individuals to certain shells, and is of a size comparable to the punctae of *Cyclopuncta*, is *Folliculina*. Species of this infusorian secrete a horny sheath or *lorica*, and are known to attach themselves habitually by the posterior of the lorica to various marine shells. Thus Kent (1882, p. 598) observed *Follicullina ampula* (Miller) "in countless numbers upon the spiral shells of the tubicolous annelid *Spirorbis nautiloides*" also two varieties of the same species "growing upon the single shell of a *Pecten*." He also observed another species, *Folliculina hirundo* Kent "attached in abundance to various marine polyzoa and seaweeds" (*ibid.*, p. 600).

According to Kent "the basis of attachment of the lorica . . . occupies a very small area of the surface, being limited entirely to the posterior region" (*ibid.*, p. 600). The illustration of the mode of group attachment

of *Folliculina ampulla* to *Spirorbis* is supplied by Stein (1867), whose sketch is republished by Lancester (1903, text-fig. 62 on p. 407). According to the measurements of the length of the body of *F. ampulla*, from .1 mm. to .4 mm., and of the body *F. hirundo*, about .13 mm., the diameter of the base of lorica seen on various sketches is of the order from .05 mm. to .1 mm., which is very close to the diameter of the smallest of our fossil punctae.

On the other hand, the students of these living infusoria give no hint as to the effect which the bases of their loricae may have on the calcareous substratum of the shells, to which they are attached. It seems worth considering, however, the possibility that their attachment is sufficiently permanent to become more or less embedded at the bases in the substance of the growing shells. A case of Carboniferous *Spirorbis* being thus embedded in the shell of some clams has been described by Trueman (1942), and there is hardly any doubt that the scars upon the shells to which *Spirorbis* is attached are not a result of boring, but were produced by a prolonged passive attachment. Thus it seems quite conceivable that a lorica-secreting infusoria related to *Folliculina*, and of only slightly larger size than its living species, could have lived in Carboniferous time and could have produced the punctae upon the shells of the cephalopods.

The examples of the attachment of the living *Folliculina* cited above apparently indicate certain selectivity of the substratum, such as *Spirorbis* by *F. ampula*, and *Pecten* by *F. hirundo*. The fact that the punctae of *Cyclopuncta* have been observed only on some cephalopods is therefore quite understandable in the light of the suggested interpretation of their nature.

The diameter of the punctae may be considered specific character of *C. girtyi*, while the general shape of the punctae and the manner of their distribution upon the shells seems rather characteristic for the genus *Cyclopuncta*.

ENCHOSTOMA (?) sp. cf. E. BICARINATUM Girty

1911. *Enchostoma bicarinatum*, GIRTY, U. S. Geol. Survey Bull. 439, p. 28–29, pl. 10, fig. 1.

1957. Flattened tube of unknown nature, Elias, Jour. Paleontology, v. 31, pl. 50, figs. 17, 18.

This enigmatic fossil serves as a core for the encrusting *Stenocladia* (?) *bassleri*, n. sp. Its shape and size is close to *E. bicarinatum* from the Moorefield shale of Arkansas. It was described by Girty as "thin flattened filaments" which "suggest grasslike leaves of sea-plant, but have the shiny phosphatic lustre of *Lingula* and *Conularia*." Specimens have subparallel sides, are up to 1.25 mm. wide, and their "two opposite sides being, as it were, stiffened and reinforced into carinae and the intermediate membrane being more tenuous and flexible" (Girty, 1911, p. 28). (See pl. 50, fig. 1g [bottom part] in part I of these four papers.)

The specimen from the Redoak Hollow is about 1 mm. wide, very slightly narrowing toward one end, and its opposite sides are only imperceptibly more inflated than the slightly sagging axial part. The fact that its substance has not been leached out, while the calcareous parts of the encrusting bryozoan are gone, proves that it is not a calcareous fossil, and its lustre resembles that of *Lingula* and *Conularia* just as Girty observed on his material. For these reasons it is tentatively compared with *Enchostoma bicarinatum*. Its nature remains as enigmatic as it appeared to Girty.

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UPPER DEVONIAN AMMONOIDS FROM THE *MANTICOCERAS* ZONE, FITZROY BASIN, WESTERN AUSTRALIA

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ABSTRACT—The ammonoid fauna of the *Manticoceras* Zone (Frasnian, or early Upper Devonian) of the Fitzroy Basin in Western Australia is described. It comprises 15 species (14 of them new) which are referred to 9 genera, including *Mesobeloceras*, n. gen. The assemblage consists of *Ponticeras discoidale*, *P. retorquatum*, *P.* n. sp., *Probeloceras alveolatum*, *Manticoceras lindneri*, *M. guppyi*, *M. cinctum*, *Hoeninghausia pons*, *Timanites angustus*, *Neomanticoceras erraticum*, *Mesobeloceras thomasi*, *Beloceras sagittarium*, *Tornoceras* (*Tornoceras*) *contractum*, *T.* (*T.*) *clausum*, and *Tornoceras* (*Polonoceras*) n. sp. One of the forms, *Beloceras sagittarium* (G. & F. Sandberger), was originally described from Germany, but large numbers of well preserved specimens are now known from Western Australia. Striking similarities between the Upper Devonian ammonoids of Australia, North Africa, Europe, and North America are demonstrated. Specimens of *Ponticeras* cf. *P. aequabile* and *Oxyclymenia* sp. from North Africa are illustrated for comparative purposes.

INTRODUCTION AND ACKNOWLEDGEMENTS

DURING the past fifteen years a considerable amount of stratigraphic work has been undertaken in the Fitzroy Basin of Western Australia. Important contributions have been made by staff members of the University of Western Australia, the Commonwealth of Australia Bureau of Mineral Resources, and several oil companies, notably West Australian Petroleum Pty., Ltd., and Caltex (Australasia) Oil Development Pty., Ltd. Large paleontological collections have accumulated, but to date few of them have received the detailed study which their fine preservation and exceptional scientific interest seem to warrant. However, Curt Teichert has made preliminary studies of practically all of the collections, and in several publications has given excellent accounts of their taxonomic composition. The Devonian ammonoid collections were assembled by Teichert, and preliminary identifications were made for most specimens. The present author first became interested in the Devonian ammonoids when serving as Teichert's Research Assistant, and during this period he prepared much of the material for study. Teichert's departure from Australia occurred before it was possible for him to embark on the formal description of the ammonoids, and the collection passed to the present author for study.

Only the ammonoids of the *Manticoceras* zone are described in the present paper. Further studies will cover the remaining younger Upper Devonian goniatites and clymenias, together with the exceptionally plentiful and well preserved conodont material found with the cephalopods. Our knowledge of the stratigraphy of the Fitzroy Basin is at present in a "state of flux," and accordingly, detailed accounts of stratigraphy and biostratigraphy will be delayed until the younger faunas are described.

It is with pleasure that the author wishes to acknowledge the assistance rendered to him by Dr. Curt Teichert, Professor Arthur K. Miller, and Professor William M. Furnish. Each has contributed in different and diverse manners, but all three have aided materially during the course of the work. Dr. Teichert collected many of the specimens, assembled the material, introduced the present author to its study, and rendered helpful advice during the writing of the paper. Professor Miller made freely available the contents of his excellent library, Professor Furnish was invaluable in advising on preparational and illustrative techniques, and both rendered advice and constructive criticism during all phases of the work.

Grateful acknowledgement is also due to the Director of the Commonwealth of Australia Bureau of Mineral Resources, and the Head of the Department of Geology of the University of Western Australia for permission to study the collections in their keep-

ing. Mr. G. A. Thomas and other members of the Bureau of Mineral Resources field parties, together with Mr. D. J. Guppy and Mr. A. W. Lindner of West Australian Petroleum Pty., Ltd., collected many of the specimens and supplied the author with much valuable stratigraphic information. Collections of ammonoids from North Africa were loaned for comparative purposes by Professor K. E. Caster of the University of Cincinnati, Professor Willard Berry of Duke University, and Drs. E. J. and D. N. Zeller, of the University of Kansas.

The paper was written in the Department of Geology of the State University of Iowa. The work was made financially possible by scholarships under the United States of America Fulbright and Smith-Mundt Acts, together with a Research Fellowship of the State University of Iowa and a Research Assistantship in the Department of Geology there.

HISTORY OF DISCOVERY

The first geologist to visit the Kimberley District was E. T. Hardmann, who worked in the area during part of 1883 and 1884. He made several small collections of fossils and these were forwarded for identification to the British Museum of Natural History. Several goniatites were included in the material, and they were later described by Foord (1890). Although the specimens were few in number, and their preservation poor, Foord correctly concluded that the containing beds were of Devonian age. His paper represents the first report of Devonian goniatites from Western Australia. Two species of "*Goniatites*" were distinguished, one "of the type of *G. rotatorius* de Koninck" and the other of indeterminate specific affinities. Both forms were from Mt. Pierre. Foord's material was too poorly preserved to permit detailed comparisons with faunas outside of Australia, but a few years later Gürich (1901) ventured the opinion that these fragmentary specimens might represent early-Upper Devonian species. His proposal has proved to be correct.

In his two reports on the Kimberley District, Hardmann (1884 and 1885) came to the conclusion that the beds which are now known to be of Devonian age should be assigned to the Carboniferous system. Those which are now thought to be of upper Precambrian age were considered to belong to the Devonian system. Intermittent field work was carried out in the Kimberley District for the next half century. However, little detailed paleontological study accompanied this field reconnaissance, and it was left to L. V. Hosking (1933) to demonstrate satisfactorily the widespread occurrence of Devonian strata in the Kimberley District. Hosking's work marked the first progress towards the understanding of the stratigraphy of the area since the occurrence of Devonian fossils was demonstrated in 1890.

Meanwhile, some attention had been given to the cephalopods of the area. Extensive collections were made in the vicinity of Mt. Pierre by Arthur Wade, and his report (1924, pl. 3) contains illustrations of seven specimens of goniatites. The "massive coral limestones" of the Rough Range, as well as the goniatite limestone of Mt. Pierre, were regarded by Wade as of Lower Carboniferous age, although he suggested that some of the lower beds were possibly Upper Devonian. It was thought that the Mt. Pierre limestone was older than that of the Rough Range. The fossils collected by Wade were examined by Frederick Chapman. In a pamphlet, apparently published slightly later than Wade's report, Chapman records five species of hydrozoans and corals from the Rough Range and "Prince's Spring" as of "Upper Devonian or Lower Carboniferous" age, and ten species of crinoids, corals, and cephalopods from Mt. Pierre as of "Middle Devonian to Carboniferous age." He noted "Various Cephalopod shells, including ammonitoid forms [such] as *Aganides* and (?) *Gonioclymenia*, and a cyrtoceracone (Nautiloid shell)." Neither of these generic identifications can be validated, but later Wade (1938) correctly identified several of the specimens in his collections as *Beloceras multilobatum*, a species now known as *Beloceras sagittarium* (G. & F. Sandberger). The first attempt at exact age determinations of the Devonian sediments of the area was made by Delépine (1935), who ably described a small collection of goniatites secured in 1927 from the Mt. Pierre district by E. de C. Clarke and H. W. B. Talbot. Delépine recorded the following species, *Sporadoceras contiguum* (Münster),

Pseudoclymenia australis Delépine, *Tornoceras* sp. nov.?, and *Dimeroceras clarkei* Delépine, and he concluded that the containing beds should be referred to the "Middle Famennian, probably to somewhere about Zone III, *Prolobites* Zone."

A one-day visit to the goniatite localities by Curt Teichert, in 1939, may be said to have initiated a new era in the investigation of the Kimberley Division Devonian sediments. From a study of his own collections and those of Wade, Teichert (1941) recorded the following ammonoids: *Beloceras multilobatum*, *Manticoceras* sp., *Tornoceras* spp., *Cheiloceras* spp., *Imitoceras* n. sp., *Dimeroceras clarkei*, *Platyclymenia* sp., *Pseudoclymenia australis*, and *Sporadoceras* n. sp.; thereby demonstrating that the equivalents of Oberdevonstufe I, II, and III were present in Western Australia. Extensive field investigations of the area were carried out by Teichert during 1940, in connection with a geological reconnaissance for Caltex (Australasia) Oil Development Pty., Ltd. Largely as a result of this work, Teichert (1943) was able to give a comprehensive account of the faunal content and distribution of the Fitzroy Basin Devonian sediments. Forty-four species were recorded from the *Manticoceras* beds (Stage I), including species of the goniatite genera *Bactrites*, *Koenenites*, *Timanites*, and *Beloceras*. The *Cheiloceras* beds (Stage II) were reported to contain a fauna consisting mainly of about twenty-five species belonging to the genera *Cheiloceras*, *Imitoceras*, *Tornoceras*, and *Dimeroceras*. The eighty-four species recorded from the *Sporadoceras* beds (Stage III) were stated to include about sixteen species belonging to the genera *Tornoceras*, *Sporadoceras*, *Dimeroceras*, *Pseudoclymenia*, and *Platyclymenia*. The one-hundred-species fauna of the *Productella* limestone (Stage IV) yielded only poorly preserved ammonoids; it was stated that *Cyrtoclymenia* was certainly present, *Platyclymenia* was probably present, and poorly preserved specimens were doubtfully referred to *Laevigites*. While considering that this Stage was probably the equivalent of the Oberdevonstufe IV, Teichert concluded that the correlation could not be regarded as having been established beyond doubt. In the course of Teichert's work some 4,000 fossils were collected from 167 different outcrops of the Middle and Upper Devonian sediments, and well over 300 species were differentiated. This work constitutes one of the major contributions to the knowledge of Australian biostratigraphy. A further paper was published by Teichert (1949), in which he recorded the observations on which the 1943 paper was based. All of the ammonoids collected by Teichert were made available to the present author for study.

Until 1948, no detailed mapping had been undertaken in the Devonian sediments of the Fitzroy Basin. All previous investigations were primarily concerned with the study of selected sections with the idea of preparing the ground for the unravelling of the complicated facies relations which prevail in the area. However, in that year field parties of the Commonwealth of Australia Bureau of Mineral Resources commenced an areal mapping project in the Fitzroy Basin. During the interval from 1948 to 1952, inclusive, mapping parties spent a total of 24 months in the field, and the remainder of the time in office preparation.

EXPLANATION OF PLATE 5

FIG. *1*—*Ponticeras* sp., figured specimen 1726, ×3½. See also Text-figs. 2C,D.

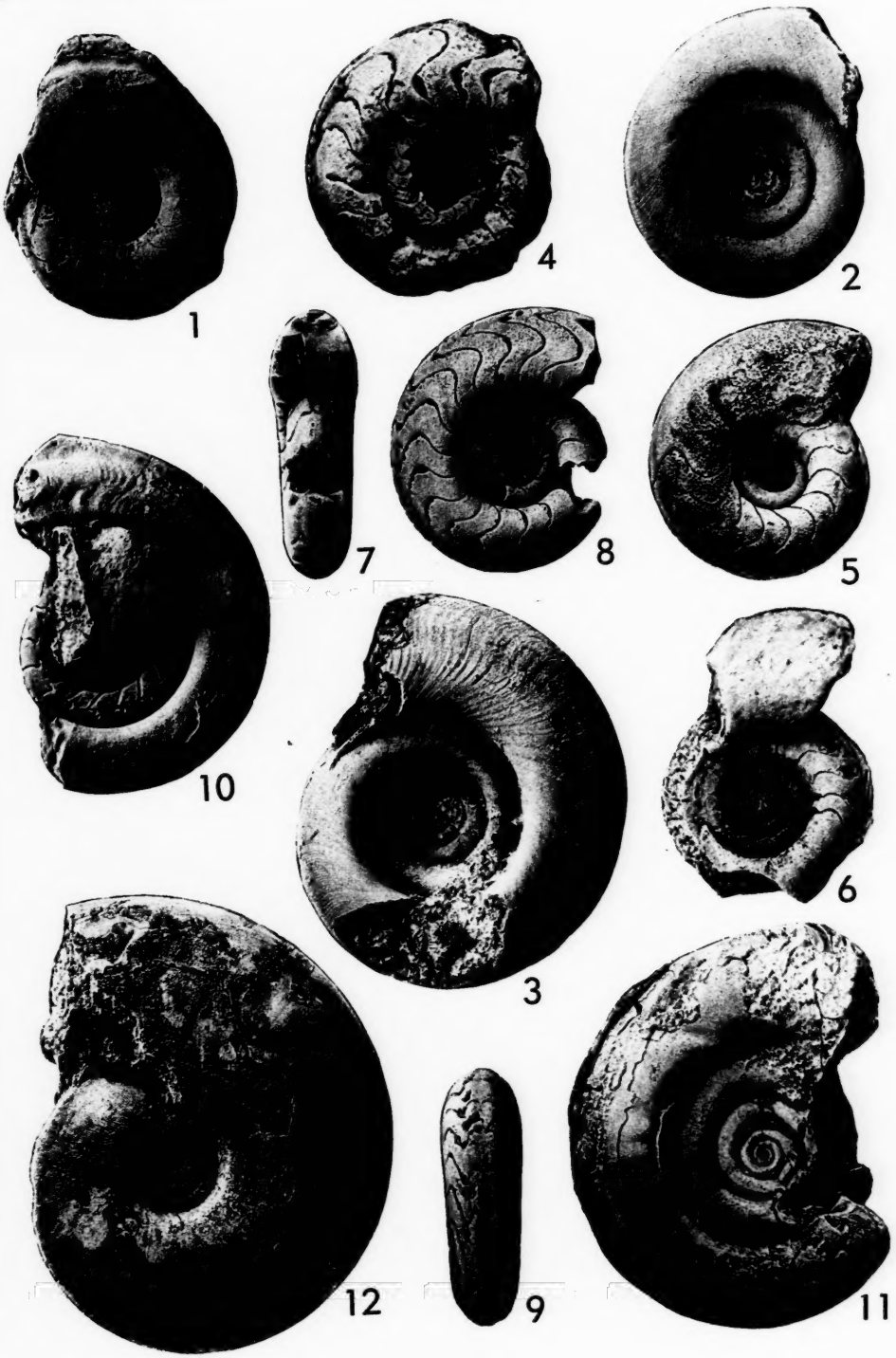
2,3—*Ponticeras retorquatum* Glenister, n. sp.; *2*, paratype 1724, ×4; *3*, holotype 1722, ×3. See also Text-figs. 1A,2B.

4–6—*Hoeninghausia pons* Glenister, n. sp.; *4*, paratype 35770, ×7; *5*, paratype 35771, ×7; *6*, paratype 35772, ×7. See also Pl. 12, figs. 5–8, and Text-figs. 8A–C.

7–9—*Ponticeras discoidale* Glenister, n. sp.; paratype 1721, ×3½. See also Pl. 12, figs. 10,11, and Text-figs. 1C,2A.

10,11—*Oxyclymenia* sp.; University of Cincinnati Museum figured specimens 31522 and 31523, respectively, from the *Gonioclymenia* Zone at Ouarourout, Algeria. *10*, ×1½, *11*, ×1¼.

12—*Beloceras sagittarium* (G. & F. Sandberger), figured specimen 1759, ×2½. See also Pl. 10, fig. 7, Pl. 13, figs. 1–5, Pl. 14, figs. 1–8, Text-figs. 13A,14,15A–E.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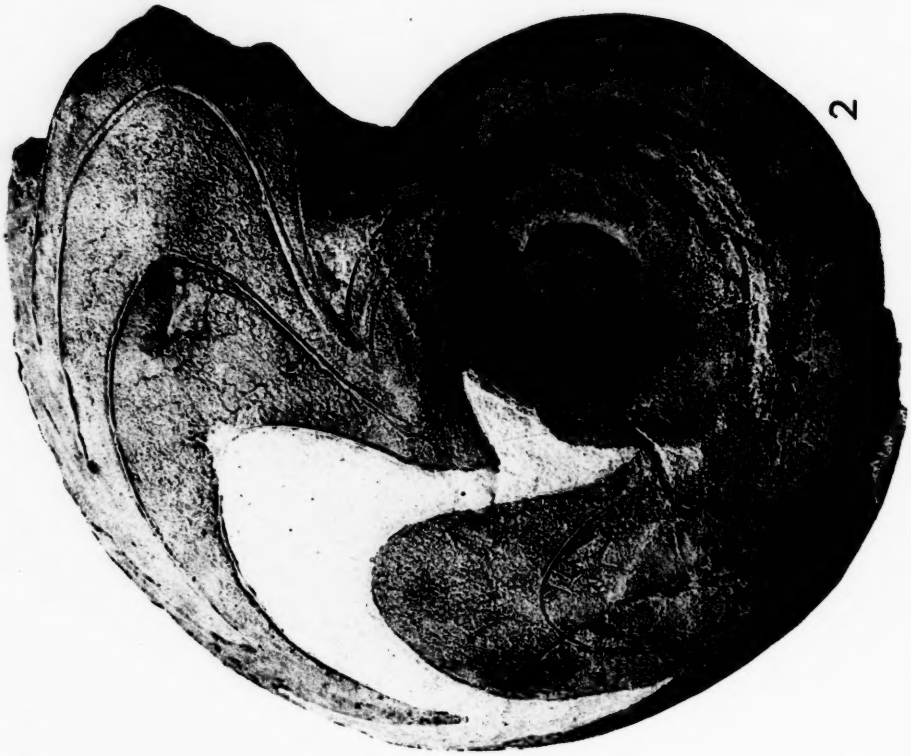

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Approximately 40,000 square miles were examined during the survey, and detailed maps covering an area of 28,000 square miles were prepared at scales of 1 inch = 1 mile, 1 inch = 2 miles, and 1 inch = 10 miles. A preliminary report was published by Guppy (1953), and the full report of the work was to follow soon after. However, at this stage the disastrous fire which severely damaged the Headquarters of the Bureau of Mineral Resources destroyed the manuscript, together with the maps and much of the assembled stratigraphic information. Fortunately, many of the fossil specimens, including the complete ammonoid collection, were in the care of Curt Teichert, and housed in the Department of Geology of the University of Melbourne.

Further field investigations were made jointly during 1953 by the Bureau of Mineral Resources and West Australian Petroleum Pty., Ltd., with the aim of repeating the work completed before the Bureau fire, and extending the survey in areal scope. No results have yet been published, so that the latest published information on the distribution of the Devonian system in the Fitzroy Basin is that given by Teichert (1942 and 1949), and by Guppy (1953). However, it is anticipated that the results of the recent investigations will be available for review in connection with the future description of the Famennian ammonoid faunas.

BIOSTRATIGRAPHIC NOMENCLATURE OF THE UPPER DEVONIAN

Throughout the present paper, frequent comparisons will be drawn between the Upper Devonian goniatites of the Fitzroy Basin and similar faunas in other parts of the world. It is therefore appropriate that attention should be directed toward the Upper Devonian goniatite successions of Germany, for they are better known than any others of comparable age and have served as a basis for world-wide comparison. A standard classification of the Upper Devonian sediments of that country has long been in use, but individual authors have modified it substantially to accommodate changing needs. The result has been a confusing terminology.

Wedekind (1926, p. 201) gave an excellent outline of the major "stages" into which the classic Upper Devonian sections of Germany were divided prior to 1938. The whole of the Frasnian formed the *Manticoceras*-Stufe I, sometimes referred to merely as Stufe I, while the Famennian was divided, from the base upwards, into the *Cheiloceras*-Stufe II, the *Prolobites*-Stufe III, the *Platyclymenia*-Stufe IV, the *Laevigites*-Stufe V, and the *Wocklumeria*-Stufe VI underlying the lowermost Carboniferous *Gattendorfia*-Stufe I. Most of these "Stufen" were subdivided into two or more "Zonen," each of the subdivisions being designated by a fossil species and the addition of a Greek letter to the "Stufen" numbers. Thus the basal portion of the *Manticoceras*-Stufe was referred to as the *Pharciceras lunulicosta* Zone Iα. Modifications were introduced by later German authors, but the basic pattern remained the same. One such change was that proposed by Matern, who in 1931 united the *Manticoceras nodulosum* Zone Iβ and the *Manticoceras cordatum* and *M. carinatum* Zone Iγ to form the *Manticoceras* Zone I(β)γ.

In Germany certain genera and species are restricted to one or more of these "Stufen" and "Zonen." Thus *Manticoceras* is not known to occur outside of Oberdevonstufe I, whereas *Timanites*, *Synpharciceras*, *Pharciceras*, *Sandbergeroceras*, and *Koenenites* are restricted to Oberdevonstufe Iα, and *Beloceras* to Oberdevonstufe I(β)γ and Iδ.

Further complications were introduced by Schindewolf (1934) when he proposed to combine Wedekind's "*Prolobites*-Stufe" and "*Platyclymenia*-Stufe." Later (*fide* Miller, 1938, p. 3) this author stated that he recognized six major divisions of the Upper Devonian, the *Manticoceras*-Stufe I, *Cheiloceras*-Stufe II, *Prolobites-Platyclymenia*-Stufe III, *Laevigites-Gonioclymenia*-Stufe IV, *Wocklumeria*-Stufe V, and *Gattendorfia*-Stufe VI;

EXPLANATION OF PLATE 6

FIG. *1,2*—*Manticoceras lindneri* Glenister, n. sp., paratype 1728, slightly less than ×1. See also Pl. 7, fig. 2, Pl. 9, figs. 1,2, Text-figs. 4,5B,C.

the last-named division is now referred to as Unterkarbon I. Thus the unsatisfactory situation arose where, for example, Oberdevonstufe IV of Schindewolf was equivalent to Oberdevonstufe V of Wedekind, Matern, and others. Of recent years the trend has been to return to the terminology of Wedekind, for Schindewolf (1952, p. 287) has referred to the *Prolobites-Platyclymenia*-Stufe III+IV. This appears to the present author as the most satisfactory method of nomenclature, and will be followed in the present work when reference is made to the European sections. "Stufen" and "Zonen" may be united, but, in effect, the original number terminology, as outlined by Wedekind (1926), is retained.

One literal translation of the German word "Stufe" is "stage," but there is an increasing tendency to restrict the term "stage" for the rocks deposited during an "age" [see Raggatt (1956) for the Australian Code of Stratigraphic Nomenclature]. In effect, the German "Stufen" are really zones, in that they are time-rock units which "contain a defined floral or faunal assemblage." The German "Zonen" are, therefore, subzones. As pointed out by Teichert (1950), the Oppelian zone more or less covers the same concept as the faunizone, florizone, and biozone, so that the use of these last three terms might well be abandoned. Several zones, *sensu stricto*, can be recognized in the Upper Devonian of Western Australia and other parts of the world. To avoid confusion when referring to the development of goniatite zones outside of Australia, it is proposed to follow Teichert (1949) in considering the German "Stufen" as zones but to retain the original German word when referring to German successions. This course of action has the obvious advantage of not implying strict contemporaneity between the goniatite zones of Western Australia and the "Stufen" of other parts of the world. It is important, for although the *Manticoceras* Zone and the *Cheiloceras* Zone of the Fitzroy Basin are homochronous with the *Manticoceras*-Stufe I and the *Cheiloceras*-Stufe II of Germany, only general correlation can at present be implied between the higher zones of the Fitzroy Basin and the higher "Stufen" of the German sections.

Teichert (1949) proposed to apply a symbol classification to the Western Australian Upper Devonian zones, using Arabic numbers and Greek letter suffixes in the same manner as the Roman numbers are used for the German Devonian. This practice seems to form a basis for future difficulties, such as were encountered in Germany, when the Western Australian zones are in need of revision. It is therefore proposed to abandon this symbol classification, and in its place to substitute zone names formed from the generic name of the zonal genus, and subzonal terms formed from either the specific or generic taxon of the subzonal species or genus. Thus the equivalent in Western Australia of *Manticoceras*-Stufe Iα of the German sections is the *Timanites angustus* Subzone, and the equivalent of *Manticoceras*-Stufe I $(\beta)\gamma$ is the *Beloceras sagittarium* Subzone. In this manner, it is anticipated that future students will be able to add to or subtract from the zones or subzones without completely rejecting the older terminology.

STRATIGRAPHIC NOMENCLATURE

At the time of writing, a comprehensive account of the geology of the Fitzroy Basin is in press (Guppy *et al.*, 1957). It is the first attempt at definition of most of the Devonian rock units in the area. The inclusion in the present work of a review of the stratigraphy of the Fitzroy Basin is thus impracticable and unwarranted. However, each of the formations which yielded Frasnian ammonoids is briefly defined and described below. All formal names for the rock units were erected by Guppy *et al.* (1957), and the following stratigraphic information is largely extracted from their work.

SADLER FORMATION

Distribution—Named for Sadler Ridge, 125° 56′E, 18° 36′ S; crops out on Sadler Ridge, Bugle Gap, Pillara and Hull Ranges, Outcamp Billy Hills, and Oscar Plateau.

Lithology—Calcarenite, sandy calcarenite, biohermal limestone.

Contacts—Overlies the Pillara Formation unconformably. Overlain conformably by Gogo Formation and Fossil Downs Formation. Some lateral interfingering with the Virgin Hills Formation.

Thickness—Variable, from 670–1,200′.

Age—Frasnian-Upper Devonian Zone I.

Ammonoid fauna—
Ponticeras discoidale
Manticoceras guppyi

GOGO FORMATION

Distribution—Named for Gogo Station, where almost all of the known exposures occur. Homestead co-ordinates are 125° 36′ E, 18° 16′ S. Crops out N. of Pillara and Emanuel Ranges, Bugle Gap, Old Bohemia Homestead area.

Lithology—Concretionary calcareous siltstone, shale, bedded limestone.

Contacts—Overlies the Sadler Formation unconformably. Overlain conformably by the Virgin Hills Formation, and may partially interfinger with it.

Thickness—1,050′ in the only complete measured section.

Age—Frasnian-Upper Devonian Zone I.

Ammonoid fauna—
Ponticeras discoidale
P. n. sp.
Probeloceras alveolatum
Hoeninghausia pons
Manticoceras guppyi
Timanites angustus
Tornoceras (*Tornoceras*) *contractum*

VIRGIN HILLS FORMATION

Distribution—Named for Virgin Hills, 125° 55′ E, 18° 33′ S; crops out in vicinity Mt. Pierre, N of Pillara Range, Virgin Hills, Outcamp Billy Hills, Bugle Gap, Old Bohemia Homestead area.

Lithology—Red-brown, grey, and mottled silty limestone; calcareous siltstone; shale; locally sandy and conglomeratic; small bioherms.

Contacts—Overlies Gogo Formation conformably, and may partially interfinger with it. Overlain conformably by the Bugle Gap Formation and Fairfield Beds. Interfingers laterally with Sadler Formation.

Thickness—Variable, from several hundred feet to 1,400′.

Age—Frasnian and Famennian-Upper Devonian Zones I–III.

Ammonoid fauna (Frasnian species only)—
Ponticeras retorquatum
Manticoceras lindneri
M. guppyi
M. cinctum
Neomanticoceras erraticum
Beloceras sagittarium
Tornoceras (*Tornoceras*) *clausum*

FOSSIL DOWNS FORMATION

Distribution—Named for Fossil Downs Station, where all known exposures occur; Homestead co-ordinates are 125° 48′ E, 18° 08′ S.

Lithology—Pink and grey calcarenite, sandy and silty limestone, limestone breccia, biohermal limestone, dolomite.

Contacts—Overlies Pillara Formation unconformably. Overlain conformably by Fairfield Beds.

Thickness—Variable, up to 1,700′ maximum.

Age—Frasnian and Famennian-Upper Devonian Zones I–III.

Ammonoid fauna (Frasnian species only)—
Mesobeloceras thomasi
Beloceras sagittarium
Tornoceras (*Polonoceras*) n. sp.

SYSTEMATIC DESCRIPTIONS

Order AMMONOIDEA Zittel, 1884
Suborder ANARCESTINA Miller & Furnish, 1954
Superfamily GEPHUROCERATACEAE Frech, 1897
Family GEPHUROCERATIDAE Frech, 1897
[*ex* Gephyroceratidae]

As interpreted by the present author, the family Gephuroceratidae includes the following genera: *Ponticeras* Matern (1929), *Probeloceras* Clarke (1899), *Manticoceras* Hyatt (1884), *Hoeninghausia* Gürich (1896), ?*Koenenites* Wedekind (1913) [possibly a synonym of *Hoeninghausia*], and *Timanites* Mojsisovics (1882). Representatives of this family are restricted to the Frasnian (early Upper Devonian) and its time equivalents.

Genus PONTICERAS Matern, 1929

Type species.—*Ammonites aequabilis* Beyrich, 1837.

This genus was established by Matern (1929, p. 151) to include species which had previously been referred to *Manticoceras* and *Gephyroceras*. As type species he designated *Ammonites aequabilis* Beyrich (1837, p. 34–35) from Zone Iα and possibly Zone I $(\beta)\gamma$ of the Upper Devonian of Germany. In that species the conch is subdiscoidal with shallowly impressed whorls and a broad umbilicus. The internal suture is unknown, but Beyrich's illustrations (1837, pl. 2, fig. 1) show the external suture to consist of a prominently subdivided trifid ventral lobe and a rounded first lateral lobe. A more nearly accurate sutural illustration was given by G. & F. Sandberger (1850, pl. 8, fig. 10b,e), and the species was again discussed by Wedekind (1918, p. 121–123). The latter author indicated that each complete suture forms a total of only four primary lobes, rather than six as in *Manticoceras*. When he founded the genus *Ponticeras*, Matern (1929, p. 151) considered that the type species developed only four primary lobes, since he referred to Wedekind's treatment of *Gephyroceras aequabile* for the generic diagnosis. Miller (1938, p. 70) also followed these

workers in his revised diagnosis of the genus, stating that "presumably the lateral saddles of the internal sutures extend across the umbilical seams to the first lateral lobes of the external sutures (as in *Prolobites*), and there are no lobes formed in the region of the umbilicus."

Ponticeras received further detailed attention in Matern's monograph on the Upper Devonian goniatites of the Dill-Mulde area (1931, p. 79–87). He referred to it the following species, *Gephyroceras pernai pernai* Wedekind (1918, p. 166–167), *Gephyroceras pernai applanata* Wedekind (1918, p. 167), *Gephyroceras barroisi* Wedekind (1918, p. 167), *Goniatites planorbis* G. & F. Sandberger (1851, p. 96–98), *Goniatites forcipifer* G. & F. Sandberger (1851, p. 81–82), *Goniatites gerolsteinensis* Steininger (1853, p. 43), *Gephyroceras sandbergeri* Wedekind (1913, p. 69), *Ammonites aequabilis* Beyrich (1837, p. 34–35), *Gephyroceras kayseri* Wedekind (1918, p. 167–168), *Goniatites prumiensis* Steininger (1853, p. 43), and a then new species, *Ponticeras sahlgrundensis*. The genus was not recognized outside of the *Manticoceras*-Stufe of Europe until Miller (1938, p. 71) described a new species, *Ponticeras stainbrooki*, from the Independence shale at Brandon, Iowa. The single known specimen on which this species is based is in a *Ponticeras* stage of development. However, it attains a maximum diameter of only 4.7 mm., and might therefore be an immature specimen of *Manticoceras*. Miller also noted that the fragmentary specimen figured by Clarke (1904, p. 344) as "*Cheiloceras* sp." may belong in *Ponticeras*.

The species listed above show variation in details of cross section, ornamentation, and suture pattern. However, they appear to be a homogeneous assemblage, and for the present are best considered as belonging to a single genus. A study of well preserved specimens from the Upper Devonian of Western Australia and Morocco necessitates a revision of the generic diagnosis. The Moroccan specimens (State University of Iowa No. 9634), from 15 km. east of Taouz, should probably be included in *Ponticeras aequabile* (Beyrich), whereas the Western Australian specimens are described below as *Ponticeras* sp., *Ponticeras retorquatum*, and *Ponticeras discoidale* Glenister, n. spp. The internal sutures of most species of *Ponticeras* have never been adequately illustrated, but all three named species just cited show them clearly (text-fig. 1). Both *Ponticeras discoidale* and the specimens referred to *Ponticeras aequabile* prove to possess a shallow rounded dorsolateral lobe at maturity, so that the complete mature suture consists of six primary lobes, the ventral lobe being prominently trifid. *Ponticeras retorquatum* does not develop a dorsolateral lobe, and so its complete mature suture consists of only four primary lobes. The internal suture of *Ponticeras* n. sp. is unknown. Only exceptionally well preserved mature specimens can be expected to show this extra lobe, and it is considered likely that further study of the species now referred to *Ponticeras* will reveal its presence in at least some advanced forms.

Future students of goniatites may find it advisable to place in separate genera those forms having four primary lobes at maturity and those having six. Little can at present be gained from this procedure, especially since the internal sutures of most of the species are unknown. It seems more advisable to expand the generic scope so as to include both four and six lobed forms.

The generic diagnosis of *Ponticeras* may be revised as follows. Conch subdiscoidal in shape and ammonitic in growth. Whorls generally rounded across the flanks and venter, but developing flattened flanks and keeled venter in some species; moderately impressed dorsally. Ornamentation generally weakly developed, growth lines biconvex. Umbilicus large, umbilical shoulders rounded. Mature suture consists of either four or six primary lobes, the ventral lobe being prominently trifid. A broad rounded lobe occurs on the dorsolateral portion of the flanks. It may be followed by a broadly rounded dorsolateral lobe, in advanced forms, or by the deep angular dorsal lobe in immature specimens and more primitive species.

The only genus which is closely allied to *Ponticeras* is *Probeloceras* Clarke (1899, p. 90–102). The type species of the latter, *Goniatites lutheri* Clarke (1885, p. 50), has a subdiscoidal conch which is only slightly impressed dorsally, so that the umbilicus is large. The earliest growth stages in this spe-

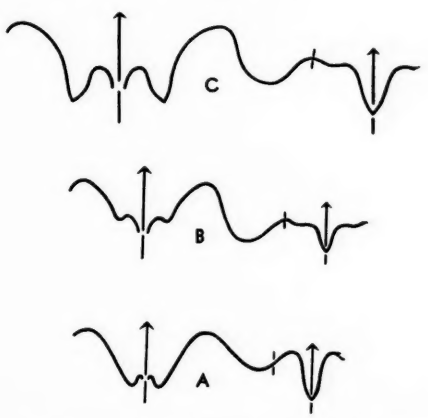
cies have whorls with rounded flanks and venter, but at a later growth stage the ventrolateral portion of the flanks becomes concave, and the venter is bicarinate. At maturity the flanks are again evenly rounded, and the venter becomes flat. Detailed study of the suture by both Clarke, and Miller (1938, p. 63), showed that at maturity it consists of only four primary lobes, the ventral lobe being trifid.

Perhaps the cross section alone is sufficient to distinguish *Ponticeras* from *Probeloceras*, for the former never develops the concave flanks and bicarinate venter of the latter. Miller (1938, p. 70) considered that the sutures of these two genera are essentially similar. The present investigations indicate the presence of two extra lobes in the internal suture of at least some mature species of *Ponticeras* and also the Australian species of *Probeloceras*. One of the species which Matern referred to *Ponticeras, Goniatites forcipifer* G. & F. Sandberger (1851, p. 81–82), seems to be better placed in *Probeloceras*. It is similar to the latter and unlike the former in having a flat venter and concave ventrolateral flanks, and in the shallowness of the impressed zone.

Ponticeras is now known from the *Manticoceras*-Stufe equivalents of western Europe, North Africa, Western Australia, and doubtfully from the Independence shale of Iowa. Matern (1931, p. 79) has demonstrated that the genus ranges from Zone Iα through Zone I $(\beta)\gamma$ of the Oberdevonstufe of western Europe.

PONTICERAS DISCOIDALE Glenister, n. sp.
Pl. 5, figs. 7–9; Pl. 12, figs. 10,11;
Text-figs. 1C,2A

Description.—Thirty-two well preserved limonitized specimens of this species are available for description. Immature whorls are broadly rounded across the flanks and venter, but bear a pair of shallow furrows situated just dorsad of the prongs in the trifid ventral lobe. These furrows bound a low flattened keel across the venter. Both the furrows and the keel become less pronounced as growth progresses, and are not found on the internal mould at overall shell diameters greater than 12 mm. At maturity each whorl is broadly rounded ventrally and flatly rounded across the flanks, so that the conch



TEXT-FIG. 1—Diagrammatic representations of sutures of *Ponticeras*. A, *Ponticeras retorquatum* Glenister, n. sp., paratype 1725, ×4, at a diameter of 18 mm.; B, *Ponticeras* cf. *P. aequabile* (Beyrich), Morocco-Clariond collection of the State University of Iowa 9634, ×3, at a diameter of 16 mm.; C, *Ponticeras discoidale* Glenister, n. sp., holotype 1720, ×3, at a diameter of 27 mm.

is subdiscoidal. The whorls are shallowly impressed dorsally, and the umbilicus is thus large. The holotype is the largest individual, with an over-all shell diameter of 27 mm., but fragmentary specimens show that the species attained measurements considerably in excess of this diameter. Several of the inner whorls of the holotype are not preserved, but it is estimated that six whorls would have been present had the specimen been fully preserved to the present diameter. Few of the specimens retain any part of the body chamber, and it is assumed that the shell material in this area was relatively weak; a maximum of slightly more than half a whorl is known to be formed of body chamber. The protoconch is small, and allows regular coiling in even the earliest-formed whorls. A runselschicht is weakly reflected on the internal mold, as are the strongly biconvex growth lines.

The mature sutures of this species consist of a total of six primary lobes and intervening saddles. The ventral lobe is prominently trifid, having pointed lingulate secondary lobes. It is bounded on each side by a broadly rounded asymmetric saddle, and a uniformly rounded lobe across the dorsolateral flanks. A low saddle, centered along the line of involution, separates the latter from a

shallowly rounded dorsolateral lobe. This is followed in turn by a deep angular dorsal lobe. The dorsolateral lobe is little more than an incipient sutural element. Although clearly shown by the holotype, it would not be observed on poorly preserved specimens and does not develop until a late growth stage.

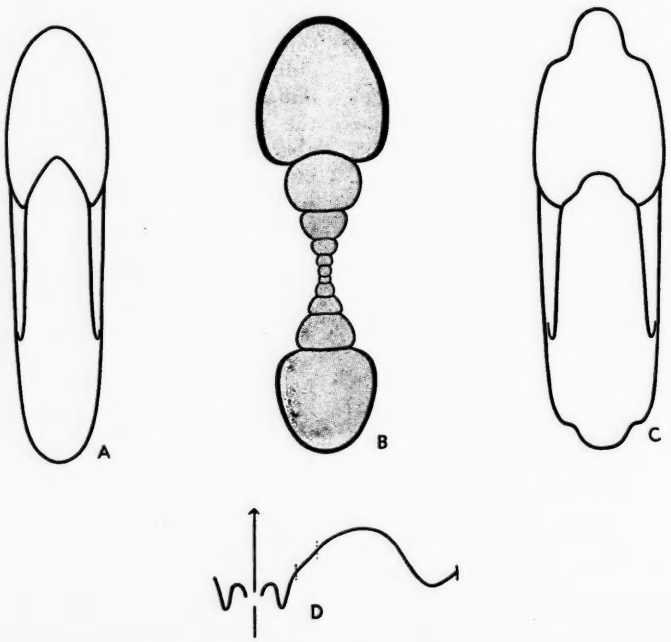
Occurrence.—NH9B (holotype), K Dup 126 (paratype), K Dud 271, K Dud 274. *Ponticeras discoidale* is found associated with the species described below as *Ponticeras* n. sp. It occurs in both the Sadler Formation and the Gogo Formation.

Repository.—Holotype 1720 and paratype 1721 are deposited with the Commonwealth of Australia Bureau of Mineral Resources in Canberra.

Comparisons.—The combination of flattened flanks and broadly rounded mature venter distinguishes *Ponticeras discoidale* from most described species of that genus. However, the species is similar in general shell form, and particularly in its wide flat umbilicus, to both *Goniatites planorbis* G. & F. Sandberger (1851, p. 96–98) and *Gephyroceras kayseri* Wedekind (1917, p. 123). The former differs in having a flattened venter, while the latter is more narrowly discoidal. The relatively wide whorls and rounded flanks which characterize the species described below as *Ponticeras retorquatum* serve to distinguish it from *Ponticeras discoidale.*

PONTICERAS RETORQUATUM Glenister, n. sp.
Pl. 5, figs. 2,3; Text-figs. 1A,2B

Description.—In addition to the type material, forty specimens of this species were available for study. Most are well preserved, and retain the shell. Immature whorls are strongly depressed and subquadrate in cross section, but as the ephebic growth stage is approached the whorls become relatively higher, and they are compressed at maturity. The whorls are subquadrate in most



TEXT-FIG. 2—Diagrammatic representations of cross sections and a suture of *Ponticeras*. A. *Ponticeras discoidale* Glenister, n. sp., holotype 1720, ×2; B, *Ponticeras retorquatum* Glenister, n. sp., paratype 1723, ×4 (line thickness accurately represents thickness of shell); C,D, *Ponticeras* n. sp., figured specimen 1726, C, ×4½, D, ×7, at a diameter of 10 mm. (dotted lines mark edges of ventrolateral groove).

growth stages, but both the umbilical and the ventrolateral shoulders are broadly rounded, with the result that the flanks appear to be rounded rather than flattened. The impressed zone is invariably shallow, and some specimens show flat or even gently convex dorsal whorl margins in the late neanic growth stage. The umbilicus is broad and shallow. Holotype 1722 is the largest known complete specimen; it has a maximum over-all shell diameter of 18.5 mm.

Growth lines are found in all ontogenetic stages. They are regular and are only weakly developed in the early stages, but become more conspicuous and less regular in mature whorls. From the umbilical seam they are directed sharply apicad. The backward sweep is reversed on the central portion of the flanks to produce a shallow saddle across the ventrolateral area. This saddle, which is little more than a flattening of the backward curvature, gives place to a broad hyponomic sinus across the venter. A portion of the aperture is preserved on the holotype.

The complete suture of mature representatives of this species forms only four primary lobes, the ventral lobe being trifid. The height of the secondary ventral saddle above either prong of the trifid ventral lobe rarely exceeds one-quarter the equivalent distance for the first lateral saddle. Each prong of the ventral lobe is narrowly rounded and gives place dorsally to a broadly rounded first lateral saddle, which traverses most of the distance to the line of involution. A shallow, gently rounded, first lateral lobe is found just ventrad from the umbilical shoulder. It is separated from a deep angular dorsal lobe by a rounded dorsolateral saddle.

The trivial name is derived from the Latin, and refers to the sharp backward sweep of the growth lines.

Occurrence.—RS 190 (all type material, numerous specimens), and R 303. This species is found associated with specimens of *Manticoceras guppyi, M. cinctum, Beloceras sagittarium,* and *Tornoceras (Tornoceras) clausum.* It is confined to the Virgin Hills Formation.

Repository.—Holotype 1722 and paratypes 1723–1725 are lodged with the Commonwealth of Australia Bureau of Mineral Resources in Canberra.

Comparisons.—The marked adapical sweep of the growth lines, and the shallowness of the impressed zone serve to distinguish *Ponticeras retorquatum* from the other described species of the genus. The external suture is similar to that of the type species, *Ponticeras aequabile,* but comparisons of the internal sutures are impossible since they are not known from the type material of that species.

PONTICERAS sp.

Pl. 5, fig. 1; Text-figs. 2C,D

Description.—A single specimen in the author's collections represents an undescribed species of *Ponticeras.* The conch is subdiscoidal. It develops a wide shallow umbilicus, and has whorls which are compressed and flatly rounded across the flanks. Two deep furrows traverse the ventrolateral flanks, and bound a prominent ventral keel. Although the keel is developed in all observed growth stages, it becomes relatively higher and more conspicuous in the living chamber. This change of cross section may indicate the mature portion of the conch, and it probably reflects the development of new living habits during the ephebic growth stage. The conch has a maximum over-all shell diameter of 12 mm., and is made up of four and a half whorls, the ultimate half whorl consisting of living chamber. Growth lines are weakly and imperfectly impressed on the internal mold. They appear to be biconvex.

The prominently trifid ventral lobe develops narrowly rounded lateral prongs. It is succeeded by a broad rounded first lateral saddle, with a scarcely discernible inflection reflecting the contours of the ventrolateral groove, and is followed by a shallow first lateral lobe just ventrad of the line of involution. Ten septa are found in the ultimate volution of the phragmocone.

Occurrence.—K Dup 126. Associated with specimens of *Ponticeras discoidale.* The species is known only from the Gogo Formation.

Repository.—Figured specimen 1726 is lodged with the Commonwealth of Australia Bureau of Mineral Resources in Canberra.

Comparisons.—Both the sutural pattern

and the whorl cross section serve to distinguish this from other Australian species of *Ponticeras*. The narrow lateral prongs of the primary ventral lobe are highly distinctive, and no other known species of the genus developed a comparable ventral keel.

There would be some justification for placing the species in *Probeloceras*, for *Ponticeras* does not typically develop grooved flanks and keeled venter. However, the concave bicarinate venter of *Probeloceras lutheri* does not resemble that of the species under discussion, and for the present the Fitzroy Basin specimen is best considered as an aberrant form of *Ponticeras*.

Two Moroccan specimens of *Oxyclymenia* sp. (University of Cincinnati Museum 31522 and 31523) are illustrated (Pl. 5, figs. 10,11) as singularly interesting examples of the development of a keel at full maturity. At the apertural end of these specimens, the cross section is similar to that of *Ponticeras* sp., but in them the prominent keel is developed only in the adapertural one-quarter of the body chamber. A deep arcuate constriction coincides with the adapical extremity of the keel, and whorls formed before this constriction are uniformly rounded across the venter. The keel of *Ponticeras* sp. has been observed at much younger growth stages, but it becomes strikingly more prominent in the mature portion of the conch. There is little doubt that the high narrow keel lodged the hyponome, whereas the constriction served to secure more firmly the animal to the inside of the conch. It seems probable that these marked morphological changes in the mature portion of the conch reflect a change in the living habits of the animal during the late ephebic growth stages.

Genus PROBELOCERAS Clarke, 1899

Type species.—Goniatites lutheri Clarke, 1885.

Clarke (1899, p. 90) coined this generic name for *Goniatites lutheri* Clarke (1885, p. 50), from the Naples group of New York, and at the same time gave an exhaustive account of a detailed study of the type species. Miller (1938, p. 63) further contributed to our knowledge of the species and summarized its characteristics as follows.

> . . . the conch is subdiscoidal but is only slightly impressed dorsally so that the umbilicus is large. During adolescence the ventral and lateral sides of the conch are rounded, but, during early maturity, concave zones are developed on the ventral side of the conch and on the ventral portion of the lateral sides; these concave zones become obsolete during late maturity. At maturity each growth-line forms a rather deep narrow ventral sinus and on either side of it a narrowly rounded ventrolateral salient, a very broad shallow broadly rounded lateral sinus; and a very small scarcely recognizable salient on the umbilical shoulder. The protoconch is subglobular, and the first volution of the conch is tightly coiled about it. At maturity each suture forms a trifid ventral lobe and on either side of it a subangular first lateral saddle, a similar but smaller first lateral lobe, and a broad broadly rounded dorsolateral saddle which extends across the umbilical seam to the more or less V-shaped dorsal lobe. Siphuncle small and ventral and almost marginal in position.

He recorded the occurrence of *Probeloceras lutheri* in the Frasnian Genesee and Naples groups of New York, Pennsylvania, West Virginia, Virginia, and Maryland.

Clarke, and Frech (1902, p. 60–61, fig. 16g), referred several other species to the genus. However, it is now apparent that none of these forms are closely comparable with *Probeloceras lutheri*. As indicated in connection with the generic discussion of *Ponticeras*, the present author is of the opinion that *Goniatites forcipifer* G. & F. Sandberger (1851, p. 81–82) is best referred to *Probeloceras*.

A single specimen in the author's collections from the Fitzroy Basin is closely comparable with *Probeloceras lutheri*. It is described below as the holotype of *Probeloceras alveolatum* Glenister, n. sp. The two

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EXPLANATION OF PLATE 7

FIG. *1—Manticoceras guppyi* Glenister, n. sp., holotype 1729, slightly less than ×1. See also Pl. 8, figs. 3,4, Pl. 10, figs. 4,5, Text-figs. 6A–D.

2—Manticoceras lindneri Glenister, n. sp., paratype 1728, slightly less than ×1. See also Pl. 6, figs. 1,2, Pl. 9, figs. 1,2, Text-figs. 3,4B,C.

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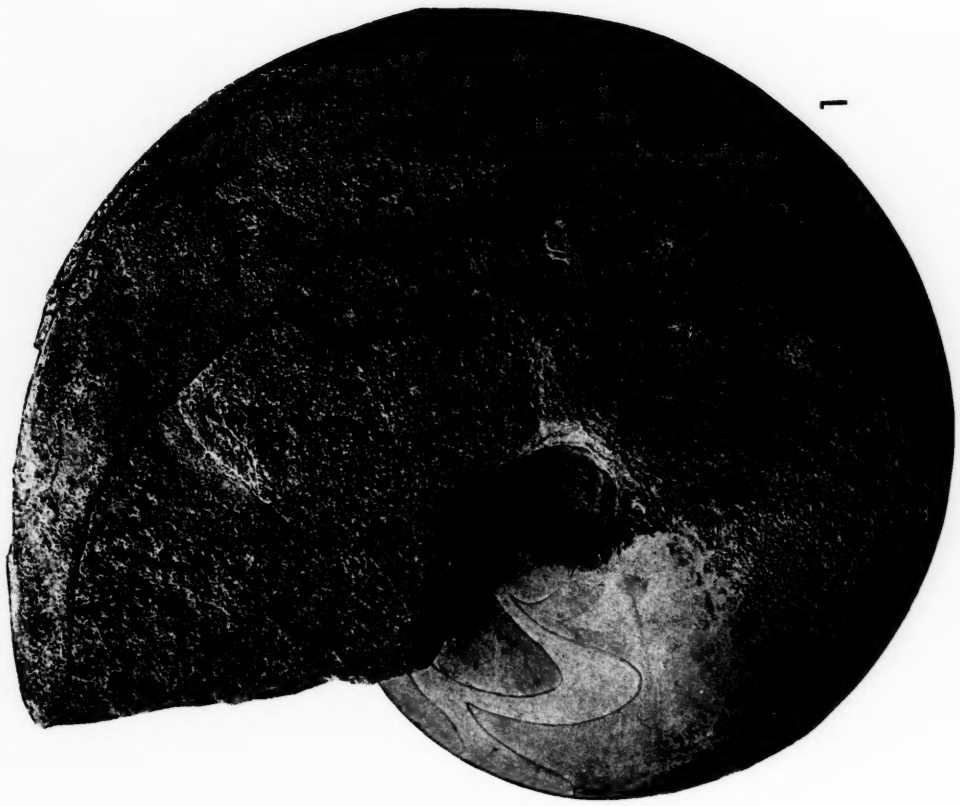

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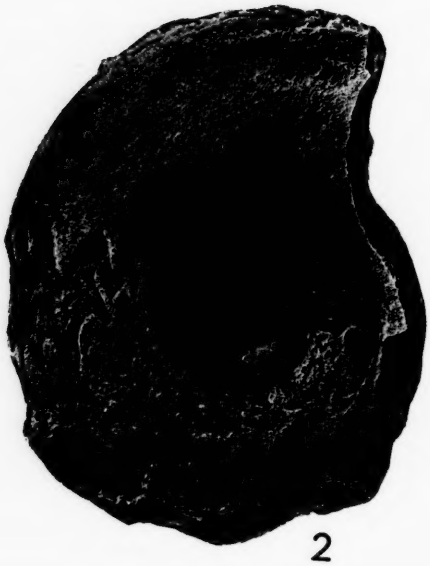

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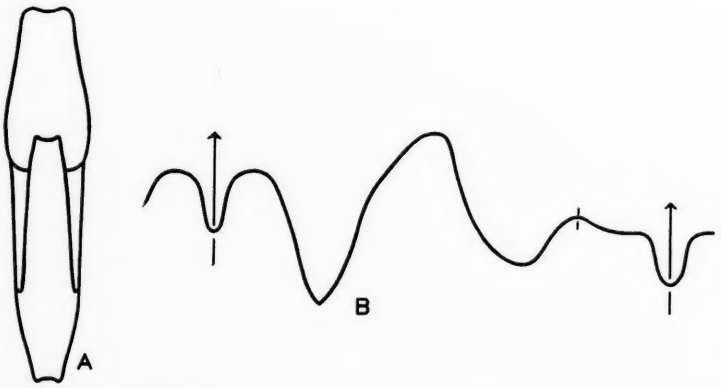

TEXT-FIG. *3*—Diagrammatic representation of cross section and suture of *Probeloceras alveolatum* Glenister, n. sp., holotype 1727. A, ×3; B, ×7, at a diameter of 13.5 mm.

species are similar in cross section and external suture, but apparently differ slightly in the internal suture. The internal suture of *Probeloceras lutheri* has not been illustrated in published accounts of the species, but a broadly rounded saddle is reported to traverse the umbilical region, and to continue directly ventrad to join the more or less V-shaped dorsal lobe. The mature suture of *Probeloceras alveolatum* bears an extremely shallow but distinct pair of incipient internal lateral lobes, and thus develops a total of six primary lobes, instead of the four reported from the type species of *Probeloceras*. The presence of this extra pair of lobes assumes greater importance when it is realized that the Fitzroy Basin specimen has a maximum over-all shell diameter of 18 mm., whereas the American species averages about 60 mm. in diameter. Some students of Devonian ammonoids may consider the additional pair of lobes warrants the erection of a new genus. However, the present author believes that this procedure would contribute nothing to our knowledge of the goniatites, whereas it would tend to obscure the extremely close affinities between the two species under consideration. Furthermore, only exceptionally preserved specimens will clearly show the internal lateral lobes. *Probeloceras alveolatum* is thus best considered as congeneric with *Goniatites lutheri*, and the generic diagnosis of *Probeloceras* should be revised to include forms in which a pair of incipient internal lateral lobes is developed.

Clarke apparently considered *Probeloceras* to be ancestral to *Beloceras*, but it is unlikely that the two forms are closely related. *Probeloceras* may be an aberrant offshoot of the *Ponticeras* lineage, or these two genera may have a common immediate ancestral stock.

PROBELOCERAS ALVEOLATUM Glenister, n. sp
Pl. 15, figs. 2,3; Text-figs. 3A,B

Description.—This species is known from a single specimen, in which the inner whorls are not preserved. However, the form of the conch is sufficiently characteristic that the species will be readily recognized when future collections are made. The conch is flatly discoidal, is subrectangular in cross

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EXPLANATION OF PLATE 8

FIG. *1*—*Mesobeloceras* sp., State University of Iowa figured specimen 9635, from the *Manticoceras* zone at Erfoud, Morocco, ×1¾.

2—*Mesobeloceras thomasi* Glenister, n. gen., n. sp., holotype 1742, ×1⅔. See also Pl. 10, fig. 6, Text-figs. 12A,B,13B.

3,4—*Manticoceras guppyi* Glenister, n. sp., paratype 1732, ×1. See also Pl. 7, fig. 1, Pl. 10, figs 4,5, Text-figs. 6A–D.

section, and develops strongly compressed whorls. The holotype has a maximum overall shell diameter of 18 mm. Each whorl is shallowly impressed dorsally, is flatly convex across the dorsolateral flanks, and is either flat or flatly concave across the ventrolateral area. It bears a shallow but conspicuous rounded groove across the venter. This ventral groove becomes progressively shallower in proportion to its width as the aperture is approached. The umbilical shoulders are uniformly rounded, and enclose a wide umbilicus. The form of the inner whorls is unknown.

One and a half whorls are preserved in the holotype, one-third of the ultimate whorl being represented by body chamber. The form of the aperture and the contours of the growth lines are unknown.

Each mature suture forms a total of six primary lobes. The ventral lobe is unequally trifid, and develops a narrow azygous secondary ventral lobe. The first lateral saddle is strongly asymmetric, and is narrowly rounded; it is followed by a broad shallow first lateral lobe, a low saddle across the umbilicus, a weakly developed incipient internal lateral lobe, and a broad dorsal lobe. The siphuncle is marginal and ventral in all observed growth stages.

The trivial name is derived from the Latin, and refers to the concave venter.

Occurrence.—The single known representative is from locality K Dup 126 in the Gogo Formation, where it is associated with specimens of *Manticoceras guppyi* and *Ponticeras discoidale.*

Repository—Holotype 1727 is lodged with the Commonwealth of Australia Bureau of Mineral Resources in Canberra.

Comparisons.—The external sutures of *Probeloceras alveolatum* differ from those of *P. lutheri* in the development of a deep secondary ventral lobe and a more gently rounded first lateral lobe. The incipient internal lateral lobe is unknown in the American species.

Genus MANTICOCERAS Hyatt, 1884

Type species.—*Goniatites simulator* Hall, 1874.

Considerable difference of opinion has developed concerning the relationship between *Manticoceras* and *Gephuroceras* [*Gephyroceras*] and the legal status of these two generic names. Both genera were proposed by Hyatt (1884, p. 316–318), the latter having page priority. By original designation the type species of *Manticoceras* is *Goniatites simulator* Hall (1874, p. 2–3), from the Upper Devonian of New York, and that of *Gephuroceras* is *Goniatites sinuosus* Hall (1843, p. 244,246), from the same general locality and horizon. These species are distinct and valid, but are obviously closely related. The single specimen figured in connection with the original description of the type species of *Gephuroceras* is fragmentary, and shows the shape of only a small portion of one of the sutures. The form of the conch, the whorl cross section and the internal sutures of the two species are closely comparable, but differences appear in the external suture. All the external lobes of *Goniatites simulator* are gently and more or less uniformly rounded, whereas those of *Goniatites sinuosus* are acutely angular. In comparing these sutures, it must be borne in mind that the maximum diameter of the holotype of *Goniatites simulator* is 45 mm., whereas the corresponding diameter for the figured syntype of *Goniatites sinuosus* is in excess of 100 mm. Comparable changes in the angularity of the external lobes have been recorded in the ontogenetic development of many adequately known species of *Manticoceras.*

From the above considerations it seems apparent that *Goniatites simulator* and *Goniatites sinuosus* are congeneric, and accordingly, either *Manticoceras* or *Gephuroceras* will have to be suppressed. The only specimen figured in connection with the original description of the type species of *Gephuroceras* is poorly preserved, and there will thus always be an element of doubt as to whether the specimens referred to this species are conspecific with the holotype. Furthermore, *Manticoceras* is more firmly established by usage, and has been widely utilized in stratigraphic terminology in many parts of the world. On the other hand, *Gephuroceras* has page priority over *Manticoceras*, and most mature individuals of species belonging to the generic group under consideration have angular sutures more like those of *Goniatites sinuosus* than those of *Goniatites simulator.* Considering all of these

factors, the present author agrees with Miller (1938, p. 72) that it will cause less confusion if *Manticoceras* be retained and *Gephuroceras* is suppressed as a subjective synonym of that generic name.

Further difficulties arise from Hyatt's questionable transliteration of the term *Gephuroceras*, for this generic name must serve, under the Copenhagen Decisions [Decision 54 (1a)], as the root for the familial taxon. Hyatt indicated that his new generic name was derived from the Greek for "a bridge," but gave the derivative as *Gephuroceras* instead of *Gephyroceras*, thereby committing an apparent solecism. This linguistic "error" was first "corrected" by Zittel (1885, p. 418), who referred to the genus as *Gephyroceras;* most subsequent authors followed the revised spelling. However, according to the Copenhagen Decisions, the original spelling must be retained. Fortunately, the generic spelling is of little importance, for *Gephuroceras* should be placed in synonymy.

In 1897 Frech established the family Gephyroceratidae, using the revised spelling, and several subsequent authors have adopted his term. Spath later drew attention to Hyatt's original spelling of the generic name and used the term Gephuroceratidae (1934, p. 19) for the first time. The only remaining alternatives were utilized by Wedekind (1913, p. 46), who proposed the subfamily Manticoceratinae and later (1918, p. 118) the family Manticoceratidae. Miller and Furnish (1954, p. 687) finally proposed the Gephuroceratacea, and retained the family name Gephuroceratidae [Gephyroceratidae] Frech, 1901.

The Copenhagen Decisions [Proposal 54 (1a)] indicate that *Gephuroceras* must serve as the valid root for the familial name, even though it be suppressed as a subjective synonym of *Manticoceras*. However, the Rules give no indication as to whether the "u" or the "y" spelling should be adopted in the formation of the familial name, as no similar case has yet been placed before the Commission. If the problem is approached from the point of view of the original generic name, then the "u" spelling, although linguistically incorrect, would be correct from the nomenclatorial viewpoint. On the other hand, it seems illogical to alter the established spelling of a familial name for the purpose of restoring a spelling error made by the author of the genus on which the family name is based.

Students of Paleozoic ammonoids would certainly be divided on which of the above alternatives is preferable. The only manner in which the problem can be satisfactorily resolved is by an application for ruling from the International Commission on Zoological Nomenclature. Until such a ruling can be established, it is proposed that:

(a) *Gephuroceras* Hyatt be suppressed as a subjective synonym of *Manticoceras* Hyatt;

(b) *Gephyroceras* Zittel be considered as an objective homonym of *Gephuroceras* Hyatt;

(c) Gephyroceratidae Frech be suppressed in favor of Gephuroceratidae Frech;

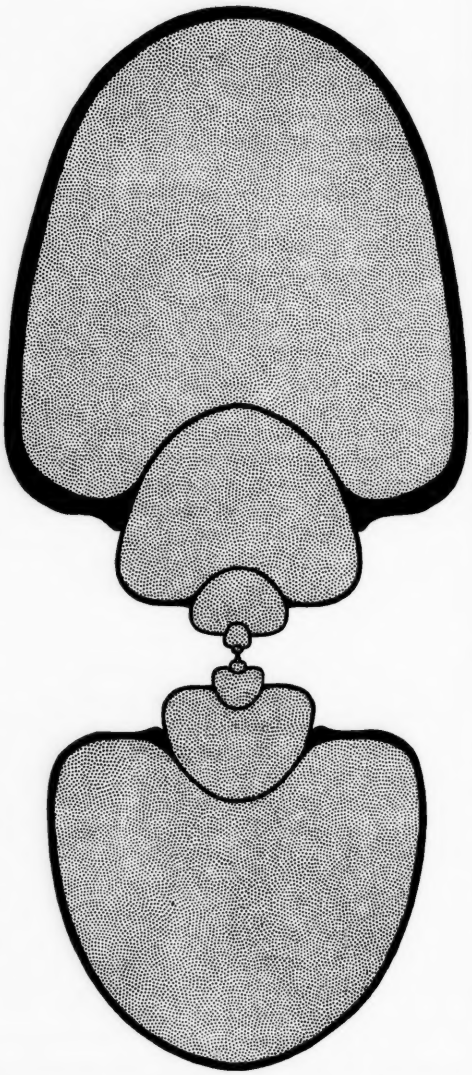
(d) Manticoceratidae Wedekind, and Manticoceratinae Wedekind be suppressed in favor of Gephuroceratidae Frech and Gephuroceratinae Frech.

The genus *Crickites* Wedekind (1913, p. 70) is closely comparable with *Manticoceras*. In his original work on the former generic group, Wedekind referred to it three species, *Crickites acutus* (G. & F. Sandberger, em. Wedekind), *Crickites exspectatum* Wedekind, and *Crickites holzapfeli* Wedekind; he later (1918, p. 130) declared the last named species as type. It is of interest to note that Matern (1931, p. 160–167) contended that the operculae described by Clarke (1884) as *Spathiocaris koeneni* were conspecific with the type species of *Crickites*, and he therefore suppressed *Crickites holzapfeli* Wedekind in favor of *Crickites koeneni* (Clarke). Subsequent authors have doubted the association suggested by Matern. The new subfamily Crickitinae Wedekind (1913, p. 170) was started to include forms whose evolution paralleled that of the Manticoceratinae, but which were distinct in possessing convex instead of biconvex growth lines. The assumption of such taxonomic importance for the growth lines is highly questionable, and has been doubted by Schmidt (1921, p. 539). Many authors agree that the development of an ocular sinus in the growth lines is a reflection of the living habits of the ammonoid animal, and is thus of only minor taxonomic significance. Furthermore, there

is extreme and apparently continuous variation in the form of the growth lines. Of the three species originally included by Wedekind, *Crickites acutus* bears strongly adorally arched growth lines across the flanks, *Crickites exspectatum* has growth lines across the flanks which, from Wedekind's illustrations, are either directly transverse or shallowly lobate (biconvex), whereas those of *Crickites holzapfeli* are shallowly arched adorally. All degrees of biconvexity have been observed in species of *Manticoceras*. Forms referred to *Crickites* have much the same stratigraphic range as those of *Manticoceras*, being known from both the Oberdevonstufe I $(\beta)\gamma$ and the Iδ. It is thus the opinion of the present author that *Crickites* Wedekind should be suppressed as a subjective junior synonym of *Manticoceras* Hyatt.

MANTICOCERAS LINDNERI Glenister, n. sp.
Pl. 6, figs. 1,2; Pl. 7, fig. 2; Pl. 9, figs. 1,2; Text-figs. 4,5B,C

Description.—Ten specimens belonging to this species, most of them in an excellent state of preservation, are available for study. All are of unusually large proportions, the largest having a maximum over-all shell diameter of 210 mm. The holotype has a corresponding diameter of 195 mm. The whorls are relatively shallowly impressed dorsally, and are flattened across the umbilical wall in such a manner that the walls of the umbilicus are nearly always perpendicular to the plane of symmetry of the conch. Umbilical shoulders have a small radius of curvature, but the flanks and venter are gently and uniformly rounded. The conch is moderately involute throughout, but it forms a deep umbilicus. Significant changes in coiling and whorl cross section appeared at maturity; these are best exhibited by the holotype. The axis of coiling changed slightly as specimens neared the mature growth stage; subsequently formed whorls encroached upon the area of the immature umbilicus. In the holotype, this encroachment starts at a position one-half of a whorl apicad of the apical end of the body chamber. The umbilical walls of the ultimate whorl of this specimen slope sharply outwards towards the axis of coiling, with the result that the umbilicus is proportionally reduced in diameter. The whorls of the holotype reach a maximum width of 85 mm., at one-quarter of a whorl apicad from the aperture; from here to the aperture the width is successively reduced, until the maximum width at the adoral end of the specimen is only 75 mm. This successive constriction of the terminal half of the



TEXT-FIG. 4—Diagrammatic cross section of *Manticoceras lindneri* Glenister, n. sp., paratype 35766, ×1 (thickness of lines accurately reflects shell thickness).

body chamber doubtless served to better secure the body of the animal within the shell, and probably reflects some change in habit as the organism reached maturity. The shell attains a maximum thickness in the vicinity of the umbilical shoulder of mature specimens, where it reaches 6 mm.

A maximum of from five to six whorls are developed, the body chamber generally occupying one-half of the ultimate whorl. The number of septa to each whorl increases at maturity, but is usually small; an immature phragmocone of 130 mm. maximum over-all shell diameter develops 14 septa in the ultimate whorl. Several specimens, including the holotype, retain a typically biconvex aperture. A deep rounded sinus is formed across the venter, and is followed by a prominent ventrolateral salient, a shallow rounded lobe across the flanks, and a low saddle across the dorsolateral flanks. Growth lines are frequently preserved across the umbilical wall; they form a shallow lobe, which is centered across the umbilical shoulder.

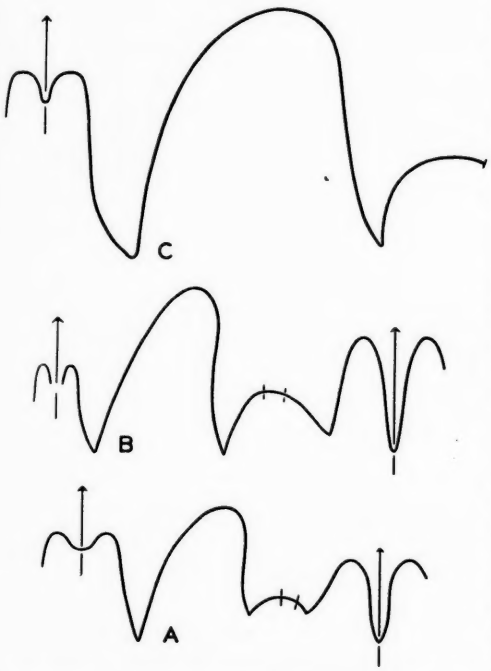
The ventral lobe is unequally trifid, for it develops a narrow rounded azygous secondary ventral lobe and a pair of deep pointed asymmetric lateral prongs. The first lateral saddle is relatively broad, especially in mature whorls, and is followed by a deep pointed asymmetric first lateral lobe, a low rounded saddle across the umbilical area, a shallow internal lateral lobe, a narrow internal saddle, and an extremely deep and narrow dorsal lobe. The first lateral saddle becomes relatively wider in mature whorls, due presumably to the rapid increase in the height of the whorls as maturity is approached.

The species is named in honor of Mr. A. W. Lindner, of West Australian Petroleum Pty., Ltd., who collected many of the specimens studied, and supplied the author with valuable stratigraphic information.

Occurrence.—C 27 (holotype), C 6–7 (paratype 35766), RS 194 (paratype 1728), C 9–10, C 17–32, K Dup 120. All known specimens are from the Virgin Hills Formation.

Repository.—Holotype 34765 and paratypes 35766, 35774, 35775, are deposited in the Department of Geology of the University of Western Australia, in Perth, and paratype 1728 is lodged with the Commonwealth of Australia Bureau of Mineral Resources in Canberra.

Comparisons.—*Manticoceras lindneri* is comparable with several of the larger species of this genus from Europe and North America. The most closely related form is *Manticoceras septentrionale* Miller, from the Carcajou Mountain sandstone, about 45 miles northwest of Norman Wells, northwestern Canada. However, this latter species differs in having shallower and more symmetrical lobes in the external suture, and in being more compressed than the Western Australian species. *Manticoceras rhynchostoma* Clarke, from the Chemung sandstone of western New York, has a strikingly similar external suture, but forms a much shallower dorsal lobe and quite a different shell cross section.



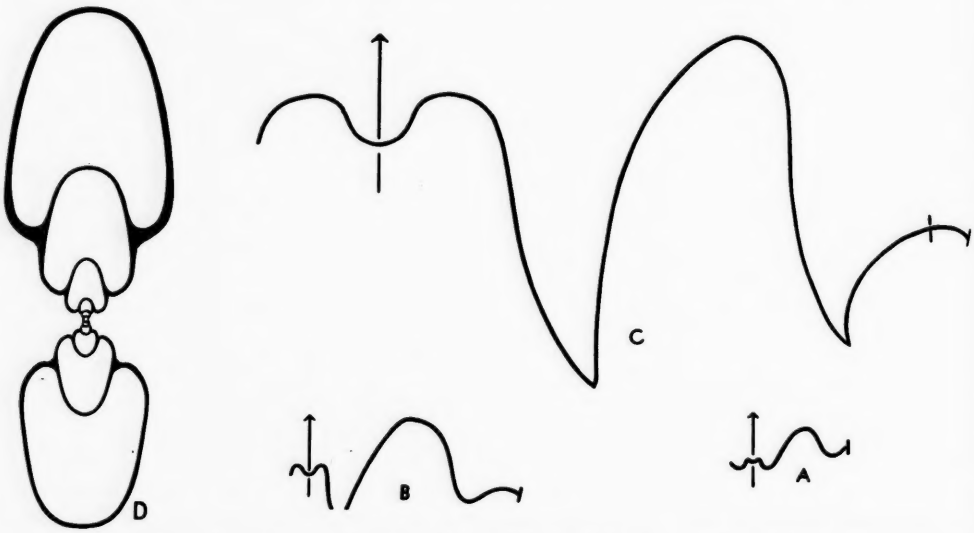
TEXT-FIG. 5—Diagrammatic representations of sutures of *Manticoceras*. A, *Manticoceras guppyi* Glenister, n. sp., paratype 1730, ×1¼, at a diameter of 38 mm.: B,C, *Manticoceras lindneri* Glenister, n. sp., B, composite drawing from paratypes 35774 and 35775, ×1, at a diameter of 75 mm., C, holotype 35765, ×1, at a diameter of 130 mm.

MANTICOCERAS GUPPYI Glenister, n. sp.
Pl. 7, fig. 1; Pl. 8, figs. 3,4; Pl. 10, figs. 4,5;
Text-figs. 5A,6A–D

Description.—This is the most prolifically represented species in the author's collections, more than 300 specimens being available for study. The largest known form is the holotype, which achieves a maximum over-all shell diameter of 135 mm., but there is a virtually complete size gradation of specimens down to 5 mm. In general, the preservation is excellent. The conch is subdiscoidal in all growth stages. The first-formed volution is depressed, but later-formed whorls become progressively narrower in proportion to their height. Mature whorls are strongly compressed, and they develop flatly convex flanks. The conch is evolute throughout; immature shells are widely umbilicate, but the umbilicus becomes proportionally narrower in larger specimens. This proportional narrowing of the umbilicus is generally associated with a slight shift in the axis of coiling, and is almost certainly a reflection of some change in living habits as the specimens reached maturity. The shell material is greatly thickened in the dorsolateral areas, especially in the vicinity of the line of involution.

A maximum of six whorls is known to be developed, slightly more than half of the ultimate whorl being represented by body chamber. Prominent lirations appear on the surface of the shell up to an over-all shell diameter of approximately 12 mm. At this size, their development was abruptly terminated, and larger specimens are either free of ornamentation or possess only indistinct growth lines. Several specimens, including the holotype, have part of the aperture preserved. Growth lines, lirae, and the aperture follow the same contours. A deep V-shaped sinus is formed across the venter, and it is flanked by a pair of high ventrolateral salients, a broad shallow lobe across the flanks, and a less prominent saddle across the umbilical shoulder.

A highly distinctive suture is developed by mature forms. The shallowly rounded azygous secondary ventral lobe is followed by a pair of low rounded secondary ventral saddles and an extremely deep asymmetric prong of the unequally trifid ventral lobe. The first lateral saddle is asymmetric and narrow, and is followed by a deep and acutely pointed asymmetric first lateral lobe a low saddle across the umbilical wall, a



TEXT-FIG. 6—Diagrammatic representations of external sutures and a cross section of *Manticoceras guppyi* Glenister, n. sp. A, paratype 1760, ×5, at a diameter of 6 mm.; B, paratype 1731, ×4, at a diameter of 16 mm.; C, holotype 1729, ×2, at a diameter of 75 mm.; D, paratype 1735, slightly more than ×1½ (thickness of lines accurately reflects shell thickness).

shallow internal lateral lobe close to the umbilical seam, an asymmetric internal lateral saddle, and a deep narrow dorsal lobe. Each of these sutural elements is maintained in even the smallest specimens observed (5 mm. over-all shell diameter), but the smaller forms have sutures with rounded lobes and more nearly symmetric sutural elements.

This species is named in honor of Mr. D. J. Guppy, of West Australian Petroleum Pty., Ltd., who collected many of the specimens studied and supplied the author with valuable stratigraphic information.

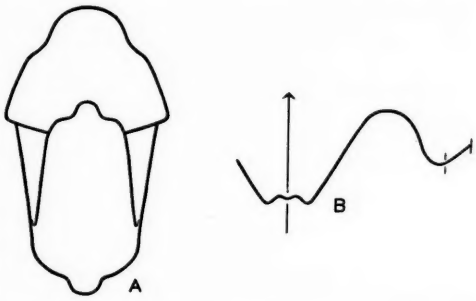
Occurrence.—RS 178 (holotype 1729), RS 190 (paratypes 1732–34), RS 190 C (paratype 1730), RS 190 D (paratype 1735), K Dup 126 (paratype 1731), RS 147, RS 181, RS 190 A–D, R 303 ?, R 304, NH 41, B 78, C 17–26, C 27, C 42, K Dud 149, K Dup 99, ? K Dup 124, ? K Dup 126, K Dup 152, K Dup 307. Typical representatives of this species were derived from the Virgin Hills Formation. However, a few small ferruginized forms are known from the Gogo Formation and the Sadler Formation. They are closely similar to immature specimens from the Virgin Hills Formation, but few of them attain an over-all shell diameter in excess of 25 mm. Future studies may prove that these small specimens from the Gogo Formation and the Sadler Formation are best placed in a separate species. However, the imperfection of their preservation and the lack of precise stratigraphic information concerning their occurrence makes such a split undesirable at present.

Repository.—Holotype 1729 and paratypes 1730–1735 are deposited with the Commonwealth of Australia Bureau of Mineral Resources in Canberra.

Comparisons.—The most diagnostic character of the species is the form of the suture, and this feature alone separates *Manticoceras guppyi* from previously described species. Particularly characteristic is the narrowness and marked asymmetry of the sutural components in the external suture. *Manticoceras regulare* Fenton & Fenton, *M. cordiforme* Miller, and *M. rhynchostoma* Clarke have only slightly less advanced sutures, but may all be readily separated from the Western Australian species by their broader first lateral saddles and more nearly symmetrical external lobes.

MANTICOCERAS CINCTUM Glenister, n. sp.
Pl. 10, figs. 1–3; Text-figs. 7A,B

Description.—This species is known from only two specimens, the larger of the two (holotype) having a maximum over-all shell diameter of 16 mm. The whorls are uniformly rounded across the flanks, but they bear a prominent rounded keel across the venter. Marked modification of the whorl cross section takes place in the ultimate quarter whorl of the holotype, the flanks becoming flattened dorsolaterally, and the keel becoming proportionally broader. The angle made by the flanks of the keel and



TEXT-FIG. 7—Diagrammatic representation of suture and cross section of *Manticoceras cinctum* Glenister, n. sp. A,B, holotype 1736, A, ×2, B, ×3, at a diameter of 8 mm.

the dorsally adjacent section of the whorl flanks also increases adorally, so that near the apertural end of the specimen the keel tends to merge into the remaining portion of the whorl. Umbilical shoulders are sharply angular, and the umbilical walls are flattened. No reasonably accurate estimate of the number of whorls present can be obtained from either specimen. The umbilicus is wide and deep, and its walls are almost vertical to the plane of symmetry of the conch.

Slightly more than one whorl of the holotype is represented by body chamber. No portion of the aperture is preserved in the holotype, but it probably lay close to the present adoral end of the specimen. Strongly biconvex lirations are developed in all observed growth stages. They form a deep rounded sinus across the keel, a narrowly rounded saddle in the grooves on either side of the keel, a broad shallow lobe across the

flanks, and a low saddle centered on the umbilical shoulder.

The sutural pattern is of a primitive *Manticoceras*-type. Externally it consists of a weakly trifid ventral lobe, a high rounded first lateral saddle, and a low rounded first lateral lobe centered just ventrad of the umbilical shoulder. Perhaps the most unusual feature of the suture is the position of the first lateral lobe, which is situated above the general sutural line. The apex of the umbilical saddle does not appear in the external suture, and it must lie close to the line of involution on the internal suture. The whorls are only shallowly impressed dorsally, and thus the internal lateral lobe will at most be only weakly developed, and it may possibly be missing.

The trivial name is derived from the Latin for "girded," and refers to the prominent keel which encircles the conch.

Occurrence.—Both specimens of this species are from locality RS 190, in the Virgin Hills Formation, where they are associated with *Ponticeras retorquatum*, *Manticoceras guppyi*, *Beloceras sagittarium*, and *Tornoceras* (*Tornoceras*) *clausum*.

Repository.—Holotype 1736 is deposited with the Commonwealth of Australia Bureau of Mineral Resources in Canberra.

Comparisons.—As far as is known, no keeled species of *Manticoceras* similar to *Manticoceras cinctum* has been described previously. The primitive nature of the suture may indicate that we are dealing with immature forms. However, the adapertural modification in cross section strongly suggests maturity.

There is some basis for placing this species in a new genus; the justification for this procedure would be greatly strengthened if future collections prove the species to lack internal lateral lobes. Even should only four primary lobes be developed, the cross section is so unlike those of species of *Ponticeras*, that it could not logically be placed in that genus. The characteristic biconvexity of the lirae, the external suture, and the general shell form suggest to the present author that the species is, at present, best referred to *Manticoceras*.

The several specimens figured by d'Archiac and de Verneuil (1842, p. 338–339, pl. 25, figs. 2–5) as *Goniatites retrorsus* von Buch may prove to be closely related to *Manticoceras cinctum*. Published illustrations leave little doubt that the figured specimens in question are quite unlike those previously referred to *Goniatites retrorsus*. The single illustration which accompanies von Buch's original description of *Ammonites retrorsus* (1832, p. 181) does not permit generic placement of the type material, but the forms referred to this species by Beyrich (1837, p. 30–31) probably belong in *Cheiloceras*. D'Archiac and de Verneuil apparently did not prepare their specimens to show the suture, for they referred only to Beyrich's description of the sutural pattern. It must therefore be concluded that the sutures of their specimens are unknown. However, in shell form, in whorl cross section, and in the form of the growth lines, d'Archiac and de Verneuil's specimens are almost indistinguishable from those of *Manticoceras cinctum*, and they are therefore referred, with reservation, to this species.

Genus HOENINGHAUSIA Gürich, 1896

Type species.—*Hoeninghausia archiaci* Gürich, 1896.

Gürich (1896, p. 348–353) proposed the genus *Höninghausia* for *Goniatites hoeninghausii* d'Archiac & de Verneuil (1842, p. 339–340) [not *Ammonites hoeninghausi* von Buch (1832, p. 172–173), which probably belongs in *Manticoceras*] and a fragmentary specimen from an unknown horizon in the Polish Mittelgebirge. He renamed the type species *Höninghausia archiaci*. This genus has, in general, been overlooked, although several species which probably belong in it have been referred to *Koenenites* Wedekind (1913, p. 28–29,47). However, Miller (1938, p. 126) concluded that the type species of the two genera "may be

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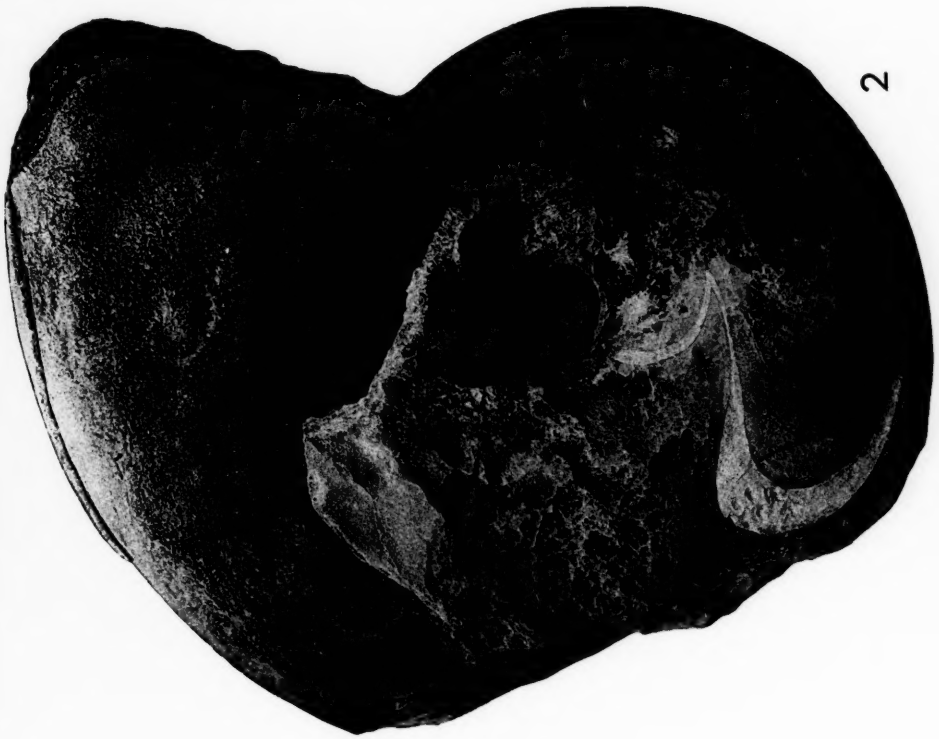
EXPLANATION OF PLATE 9

FIG. *1,2*—*Manticoceras lindneri* Glenister, n. sp., holotype 35765, ×¾. See also Pl. 6, figs. 1,2, Pl. 7 fig. 2, Text-figs. 4,5B,C.



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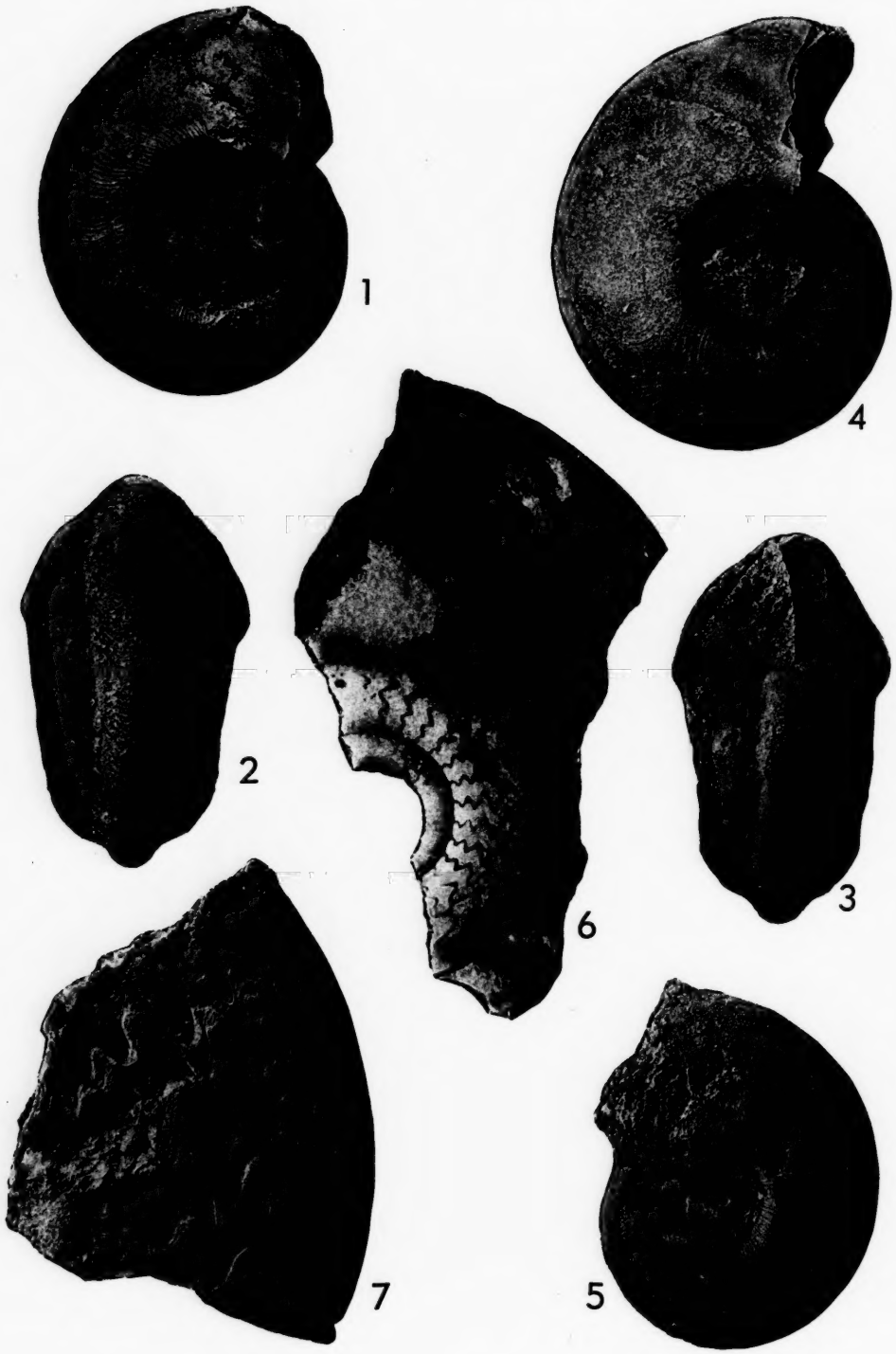
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congeneric," and that they differ only in that *Koenenites* developed a rounded venter, whereas *Hoeninghausia* forms an acutely angular ventral margin.

When proposing *Koenenites*, Wedekind referred to it two species, *Goniatites lamellosus* G. & F. Sandberger, of the Upper Devonian of Germany and France, and *Goniatites sublamellosus* G. & F. Sandberger, of the Upper Devonian of Germany. He later (1918, p. 126) designated *Goniatites lamellosus* as type species. Frech (1902, p. 59–60) considered this species to be a synonym of *Ammonites hoeninghausi* von Buch, but the two species are probably not even congeneric. Matern (1931, p. 73–76) redescribed both *Koenenites lamellosus* and *K. sublamellosus* from the Adorfe-Stufe (Iα), and added a new species, *K. galeatus*. Finally Miller (1938, p. 126–130) added another new species, *K. cooperi*, from the Squaw Bay limestone at Partridge Point, Michigan.

The internal suture of the type species of *Hoeninghausia* is unknown, but as far as can be ascertained from published figures, the external sutures of *H. archiaci* are identical with those of *Koenenites lamellosus*, except that they are slightly more advanced; certainly the differences are not of generic rank. Differentiation of the two genera can thus only rest on differences in cross section. The type species of *Hoeninghausia* has an acutely angular venter, whereas *Koenenites lamellosus* and the strikingly similar *K. cooperi*, and *K. sublamellosus* are rounded across the venter. *K. galeatus* Matern has an angular venter, and thus clearly belongs in *Hoeninghausia*. The Fitzroy Basin species, described below as *H. pons* Glenister, n. sp., is morphologically intermediate, for it develops an acutely angular venter at maturity after having a rounded ventral margin in all previous growth stages. This fact emphasizes the obvious difficulty in maintaining both *Koenenites* and *Hoeninghausia* as separate valid genera.

As further information on Upper Devonian ammonoids accumulates, it is apparent that a single channel pattern of evolution marks the development from *Ponticeras*, through *Manticoceras*, to *Timanites*. The variation is virtually continuous, and the generic stages separated out must be arbitrarily chosen and artificially defined. There is no question of natural units in this continuous succession, but rather one of convenient taxons. Complete gradation between the rounded venter of typical *Koenenites* and the angular ventral outline of *Hoeninghausia* has been demonstrated. In the opinion of the present author, there is little to be gained in maintaining the two genera. Unfortunately, the internal suture of *H. archiaci* is unknown, although there can be no reasonable doubt that it is closely similar to that of *K. lamellosus*. If the internal suture of *H. archiaci* is eventually proven to conform to the expected pattern, then *Koenenites* must be suppressed as a junior synonym of *Hoeninghausia*. However, until this sutural pattern is determined, it may be best to retain *Koenenites* for species in which the mature venter is rounded. As at present understood, *Koenenites* includes *K. lamellosus*, *K. sublamellosus*, and *K. cooperi*, while *Hoeninghausia* contains *H. archiaci*, *H. galeata*, and the new Fitzroy Basin species *H. pons*.

The relationships between *Hoeninghausia* and *Timanites* will be considered in connection with the latter genus.

HOENINGHAUSIA PONS Glenister, n. sp.
Pl. 5, figs. 4–6; Pl. 12, figs. 5–8; Text-figs. 8A–D

Description.—Sixty well-preserved limonitized specimens of this species are available to the author for description. The largest

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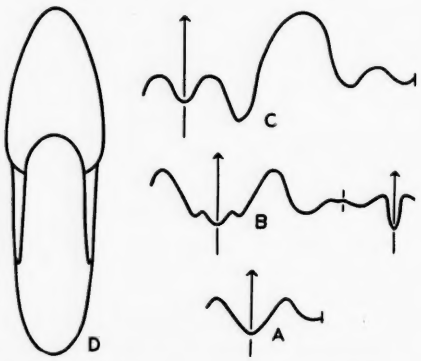
EXPLANATION OF PLATE 10

FIGS. *1–3—Manticoceras cinctum* Glenister, n. sp., holotype 1736, ×3½. See also Text-figs. 7A,B.
4,5—Manticoceras guppyi Glenister, n. sp.; *4*, paratype 1733, ×3¾; *5*, paratype 1734, ×3¾. See also Pl. 7, fig. 1, Pl. 8, figs. 3,4, Text-figs. 6A–D.
6—Mesobeloceras thomasi Glenister, n. gen., n. sp., paratype 1745, ×3½. See also Pl. 8, fig. 2, Text-figs. 12A,B,13B.
7—Beloceras sagittarium (G. & F. Sandberger), figured specimen 1752, ×1½. See also Pl. 5, fig. 12, Pl. 13, figs. 1–5, Pl. 14, figs. 1–8, Text-figs. 13A,14,15A–E.

has an over-all shell diameter of 24 mm., but the average diameter is about that of the holotype, 15 mm. Early-formed whorls are depressed, and are fairly uniformly rounded across the flanks and venter. As maturity is approached the whorls become compressed, developing flatly rounded flanks and a narrowly rounded venter. Fully mature forms are represented by numerous fragments, and these show the mature venter to be sharply angular. The whorls are shallowly



TEXT-FIG. 8—Diagrammatic representations of sutures and a cross section of *Hoeninghausia pons* Glenister, n. sp. A, paratype 35771, ×6, at a diameter of 2.5 mm.; B, paratype 35776, ×6, at a diameter of 5 mm.; C,D, holotype 35767, C, ×6, at a diameter of 10.5 mm., D, ×3.

impressed dorsally, and form a wide umbilicus. All observed growth stages have the siphuncle in a ventral marginal position.

From four to five whorls are developed by mature specimens, slightly more than half of the ultimate whorl being represented by body chamber. Eighteen septa occur in the ultimate whorl of the phragmocone in the holotype, the maximum diameter of that whorl being 10.5 mm.

Growth lines are weakly reflected on the internal mold. They are strongly biconvex, and form a deep sinus across the venter, a high salient in the ventrolateral area, a broad shallow sinus across the flanks, and a low rounded saddle centered on the umbilical shoulder.

The mature suture consist of eight lobes and intervening saddles. The ventral lobe first becomes trifid at an over-all shell diameter of 3 mm., whereas the second lateral lobe appears just ventrad of the line of involution, at a diameter of 5 mm.

The trivial name is derived from the Latin for "a bridge," and refers to the intermediate position of this species between *Hoeninghausia* and typical *Koenenites*.

Occurrence.—C 56 (holotype 35767 and paratypes 35768–35770, 35775), D 14 (paratypes 35771, 35772), D 5. All known representatives are from the Gogo Formation.

Repository.—Holotype 35767 and paratypes 35768–35772, 35775 are lodged with the Department of Geology of the University of Western Australia in Perth.

Comparisons.—Hoeninghausia pons has a sharply angular mature venter, and is thus similar in cross section to *H. archiaci*. The two species may be readily separated by the more advanced suture of the latter. *H. galeata* is almost identical with the Australian species as regards external suture and mature cross section. However, the German species developed the angular venter at an earlier ontogenetic stage than *H. pons*. *Koenenites cooperi* is similar, but although it develops flattened flanks and narrowly rounded venter, it apparently does not become angular across the ventral area at full maturity.

All specimens referred to *Koenenites* cf. *K. cooperi* Miller by Teichert (1943, 1949) are included by the present author in *Hoeninghausia pons*.

Genus TIMANITES Mojsisovics, 1882

Type species.—? *Timanites keyserlingi* Miller, 1938.

In his classic work on the "Cephalopoden der Mediterranen Triasprovinz," Mojsisovics (1882, p. 183–184) introduced the generic name *Timanites*, but gave no adequate description of the forms he intended this genus to include. The only species mentioned was *Goniatites acutus* Münster, and there is a reference in a footnote ("Vgl. Keyserling, Wissensch. Beob. auf. einer Reise in das Petschora-Land. St. Petersburg, 1846, S. 280, Taf. XII, Fig. 6") to a description and illustration of a specimen incorrectly referred by Keyserling to this species. Keyserling's specimen from the Upper Devonian of the Timan Mountains of northern Russia, was later described by Holzapfel as "*Timanites acutus* Münster" (see reproductions of

illustrations in Miller, 1938, pl. 29, figs. 1–3). However, it is readily apparent, from the illustrations, that this species is not related to *Goniatites acutus*, which is known to belong to *Cheiloceras*, but is typical of the group to which the name *Timanites* has been applied by recent authors. The species was thus without a valid name, and Miller (1938, p. 130) proposed for it the specific name of *Timanites keyserlingi*, indicating that it should be considered as the type species of *Timanites*.

According to Opinion 168 of the International Commission on Zoological Nomenclature, there is a case for considering *Goniatites acutus* Münster as the legal type species of *Timanites*. As indicated above, this species is a representative of *Cheiloceras;* if the Opinions are strictly followed, *Cheiloceras* becomes a junior synonym of *Timanites*, for it was not established until 15 years later (Frech 1897). However, it might well be argued that Mojsisovics "based his genus upon certain definite specimens [or illustrations and descriptions of them] rather than upon a species." Fortunately the best procedure to be followed in the future is the same, irrespective of which of the above lines of reasoning is preferred. To adhere strictly to the original designations would only result in unnecessary confusion surrounding two well-known genera. A decision by the I.C.Z.N. would settle the case; until such a ruling can be made it is proposed that the following course of action be followed:

(a) *Cheiloceras* should be considered as a valid genus with *Goniatites subpartitus* Münster (1839) as a type species.

(b) *Timanites keyserlingi* Miller (1938) should be considered as the valid type species of *Timanites*.

Considerable uncertainty also surrounds the relationship between *Timanites* and *Hoeninghausia* Gürich, 1896. In 1889, Holzapfel described and illustrated excellent specimens of *Timanites keyserlingi*, together with a congeneric form for which he coined the name *Timanites stuckenbergi*. Also, in accordance with a letter he received from Gürich, he included the specimens described by d'Archiac and de Verneuil (1842, p. 341–342, pl. 25, fig. 7,7a,7b) under *Goniatites hoeninghausii* von Buch, together with a worn specimen from the Polish Mittelgebirge, in the synonymy of the type species of *Timanites*. Later Gürich (1896, p. 348–350) proposed the new genus *Höninghausia* with *Goniatites höninghausi* d'Archiac and de Verneuil [not *Ammonites hoeninghausi* von Buch] as type species, renaming the species *Hoeninghausia archiaci*. At the same time he referred to this species the worn fragment from an unknown horizon in the Polish Mittelgebirge. Apparently Holzapfel intended to include in the synonymy of the genotype of *Timanites* only the worn Polish specimen, which probably represents a new species of *Timanites* that has not yet received a valid specific name.

The internal suture of *Hoeninghausia archiaci* still remains unknown. Gürich showed an internal suture consisting of two pairs of internal lateral lobes in his original publication. However, he makes it clear that he had never seen the internal suture, so that his interpretation is of little value. However, d'Archiac and de Verneuil's figures are excellent, and they show a similarity between the external suture of *Hoeninghausia archiaci* and those of all the known species of *Timanites*, including the Western Australian forms described below. The only noticeable difference is that a lobe is developed along the line of involution in all known mature specimens of *Timanites*, whereas d'Archiac and de Verneuil's figures show that the corresponding lobe in their specimen would fall in the dorsal portion of the internal suture. Such differences might well be a function of ontogenetic development. However, significant differences do appear in the coiling of the two forms. All the known species of *Timanites* are involute at maturity, and develop closed umbilici. The type of *Hoeninghausia* is moderately evolute, and the diameter of the mature umbilicus of the holotype measures one-fifth that of the over-all shell diameter. This feature alone suggests to the present author that the two genera should remain separate. However, there can be no doubt that they are closely related.

TIMANITES ANGUSTUS Glenister, n. sp.
Pl. 11, figs. 1–5; Pl. 12, fig. 9; Text-fig. 9

Description.—Twelve mature specimens and twenty immature representatives of this species are available to the author for

study. Most of the mature specimens are fragmentary, but the immature forms are more nearly complete, for they are silicified and were released from a limestone matrix. Mature specimens are narrowly lenticular, the flanks being flatly convex and the venter sharply angular. A study of the numerous immature specimens shows that the first three whorls are uniformly rounded in cross section, the angular venter first being developed in the fourth whorl. These immature specimens are evolute, and show a wide umbilicus with a large protoconch projecting above the general level of the umbilical floor. The coiling is oval for the first two whorls, but later becomes uniformly spiral. After the third whorl, at a conch diameter of approximately 5 mm., each whorl begins to overlap the one which precedes it. The umbilicus thus narrows, and the conch becomes involute. Mature specimens have a closed umbilicus. None of the larger specimens in the author's collection shows completely preserved dorsolateral shoulders. However, it appears that the ephebic whorls are impressed dorsally to a depth equal to slightly less than one-half of the height of the whorl. The siphuncle is ventral and marginal down to the smallest observed conch diameter.

The mature suture of *Timanites angustus* consists of ten primary lobes, the ventral lobe being prominently trifid. The broad first lateral saddle is asymmetric, and is followed by a deep narrow asymmetric first lateral lobe. The second lateral lobe is broader and shallower than the first, and is flanked on either side by a rounded saddle. A broad angular lobe is centered on the umbilical seam, and is succeeded by a similar but deeper interral-lateral lobe. The dorsal lobe is narrow and deep.

Most of the known specimens of this species are internal molds, so that no information concerning the ornamentation is available. However, there are suggestions that the shell was free of conspicuous ornament.

Occurrence.—RS 205 (all types), K Dup A 95, K Dup A 96. The species is found in association with *Tornoceras* (*Tornoceras*) *contractum*. It is restricted to the Gogo Formation.

Repository.—Holotype 1737, and paratypes 1738–1740 are lodged with the Commonwealth of Australia Bureau of Mineral Resources in Canberra.

Comparisons.—*Timanites angustus* is comparable with both *Timanites keyserlingi* Miller (1938, p. 130) and *Timanites occidentalis* Miller and Warren (1936, p. 634–635), but may be distinguished from these two species by its more narrowly lenticular whorl cross section. The characteristic asymmetry of the first lateral lobe is closely similar to that of *Timanites occidentalis*.

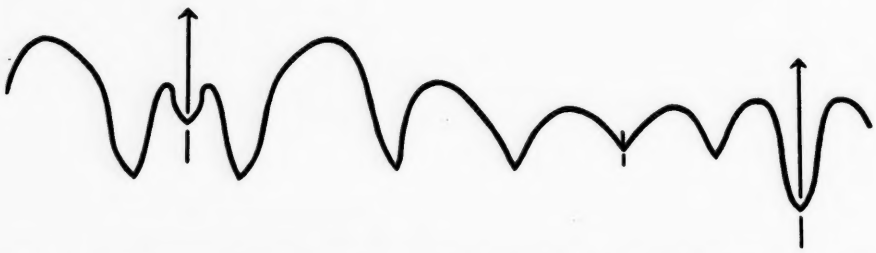
Family BELOCERATIDAE Frech, 1897

The family Beloceratidae, as interpreted by the present author, includes the following genera; *Neomanticoceras* Schindewolf (1936), *Eobeloceras* Schindewolf (1936), *Mesobeloceras* Glenister, n. gen., and *Beloceras* Hyatt (1884). It is restricted to the Frasnian (early Upper Devonian).

Genus NEOMANTICOCERAS Schindewolf, 1936

Type species.—*Manticoceras paradoxum* Matern, 1931.

In erecting this genus, Schindewolf (1936, p. 690) referred to it two described species, *Manticoceras paradoxum* Matern (1931, p. 63–64) from the Adorf-Stufe at Büdesheim in the Eifel, and *Probeloceras? naplesense*



TEXT-FIG. 9—Diagrammatic representation of the complete suture of *Timanites angustus* Glenister, n. sp., holotype 1737, ×2, at a diameter of approximately 60 mm.

Clarke (1899, p. 105) from the Naples group at Naples, New York. Also included were the specimens which Frech (1902, p. 55, Text-fig. 16g) compared with *Beloceras iynx* Clarke. Unfortunately, all of the material is poorly preserved, and is thus subject to varying interpretations of morphology. The type species is known from extremely small and presumably immature specimens, whereas *Probeloceras? naplesense* is known from a single specimen which is so strongly crushed laterally that it has almost no relief. However, Schindewolf also reported the discovery of mature specimens which he considered to be conspecific with the adolescent forms from Büdesheim, and indicated that their sutures were similar to those of *Probeloceras? naplesense* and the specimens which Frech compared to *Beloceras iynx* Clarke. No additional illustrations accompanied the work.

It is readily apparent that neither of the species referred to *Neomanticoceras* is adequately known, and that considerable uncertainty must thus exist as to the definition and delimitation of this genus. From the information available in the literature, and from a study of the holotype of *Neomanticoceras naplesense*, Miller (1938, p. 135) was able to give the following diagnosis of the genus.

"Conch sublenticular and ammoniticonic. Whorls flattened laterally and impressed dorsally. Umbilicus rather large. Growth-lines form broad, very shallow lateral sinuses, subangular ventrolateral salients, and a deep ventral sinus. At maturity each external suture forms a very broad ventral lobe (which is subdivided into five smaller lobes) and on either side of it two saddles and one lobe. Presumably, the siphuncle is ventral and marginal in position."

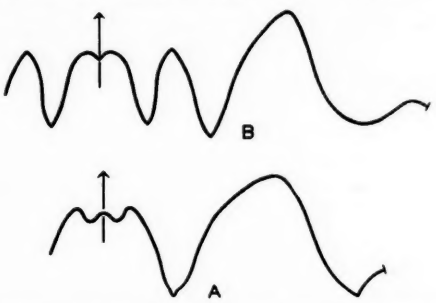
Six specimens from the *Manticoceras* Zone of the Fitzroy Basin are described below as belonging to a new species, *Neomanticoceras erraticum*, and this species is referred with reservations to Schindewolf's genus. The Western Australian specimens have a strikingly similar cross section to that of *Neomanticoceras paradoxum*, and they share the same distribution of external sutural elements. However, important differences appear in the shape of the saddles and lobes. These differences may be largely due to the stage of ontogenetic development reached by the various specimens. Until better study material can elucidate the sutural ontogeny of the species referred to *Neomanticoceras*, the exact relationships of these species will remain uncertain. In the meantime, the Western Australian species is tentatively referred to this genus.

NEOMANTICOCERAS ERRATICUM
Glenister, n. sp.

Pl. 11, figs. 6–9; Text-figs. 10A,11

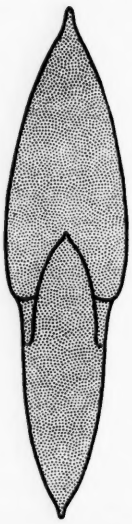
Description.—The holotype and five other mature representatives of this species are known to the author. Four of the specimens are fragmentary portions of phragmocones from which the shell has been removed, but the remaining specimens are almost complete and still retain parts of the shell. The conch is lenticular, each whorl being conspicuously compressed. Immature whorls exhibit an evenly rounded venter, but as maturity is approached the venter becomes more narrowly rounded and a ventral keel is developed. This keel is the result of local thickening of the shell; it is bounded by gently concave ventrolateral zones. Mature whorls are impressed dorsally to approximately one-quarter of their height. The umbilical shoulders are narrowly rounded, and the umbilicus is relatively narrow. In all observed growth stages the siphuncle is situated close to the base of the keel.

The inner volutions are not well preserved in any of the known specimens, but it seems probable that ephebic individuals developed at least five whorls. The present adoral margin of the holotype appears to be close to



TEXT-FIG. *10*—Diagrammatic representations of sutures of *Neomanticoceras*. A, *Neomanticoceras erraticum* Glenister, n. sp., holotype 1714, ×4, at a diameter of 40 mm.; B, *Neomanticoceras naplesense* (Clarke), ×1½, at a diameter of approximately 30 mm. (adapted from Clarke).

the aperture; two-thirds of the last whorl of this specimen is represented by body chamber. Early whorls increase uniformly in height, but the body chamber of mature individuals exhibits an unprecedented rate of increase in the height of the whorl. This results in an apparent elongation of the body chamber, and gives the impression that the latter curves away from the phragmocone. Such a shell form has obvious advantages for a motile organism, and together with the sharp venter strongly suggests that this species was an active swimmer.



TEXT-FIG. *11*—Diagrammatic representation of a cross section of *Neomanticoceras erraticum* Glenister, n. sp., holotype 1714, ×1½.

The mature external suture consists of two pairs of primary lobes, and intervening saddles. The ventral lobe is divided by four adventitious lobes, with a low saddle across the venter. A shallow rounded lobe flanks the low rounded mid-ventral saddle on either side, and it is succeeded by a low saddle and a deep attenuated lobe. The first lateral saddle is broad, but narrowly rounded, whereas the first lateral lobe is shallow and pointed.

The name is derived from the Latin for "wandering" and refers to the author's interpretation of a mobile habit for this species.

Occurrence.—RS 178 (holotype), RS 181, and RS 190 A. The species is found associated with *Ponticeras retorquatum*, *Manticoceras guppyi*, *M. cinctum*, *Tornoceras* (*Tornoceras*) *clausum*, and *Beloceras sagittarium*. It is restricted to the Virgin Hills Formation.

Repository.—Holotype 1741 is lodged with the Commonwealth of Australia Bureau of Mineral Resources in Canberra.

Comparisons.—In comparing *Neomanticoceras erraticum* with similar species, it must be remembered that slight differences in the ventral cross section of these compressed forms will produce considerable variations in the sutural pattern, even though the contours of the septa remain constant. Further difficulties result from the almost complete lack of information concerning the ontogenetic development of comparable species. In shell form, and in the remarkable extension and angularity of the living chamber, the Fitzroy Basin species is closely similar to *N. paradoxum*, the type species of the genus. However, the figured Büdesheim specimens are only a fraction of the size of those from Western Australia, and detailed comparisons are thus impossible. The sutures are generally similar to those of *N. naplesense* and to those figured by Frech (1902, p. 55, Text-fig. 16g) but are clearly more primitive than in either of these species. *Manticoceras oxy* Clarke (1899, p. 77–78), from the Chemung group of New York, is one of the few Devonian goniatites which bears a keel similar to that of *N. erraticum*. Both species have a comparable umbilicus and are strongly compressed, but the New York species lacks a second pair of adventitious lobes.

Genus MESOBELOCERAS Glenister, n. gen.

Type species.—*Mesobeloceras thomasi* Glenister, n. sp.

Diagnosis.—Moderately large, thinly discoidal ammonitocones with wide umbilici. Whorls strongly compressed, with flattened flanks and flat narrow venter at maturity; shallowly impressed dorsally. Growth lines form a ventrolateral salient and deep ventral sinus. Septa closely spaced. Mature suture contains twelve or less pairs of lobes plus dorsal lobe. Primary ventral lobe subdivided into three pairs of adventitious lobes at maturity; up to nine lobes separate first lateral saddle from deep dorsal lobe. Sutural elements have similar characteristic shape to those of *Beloceras*.

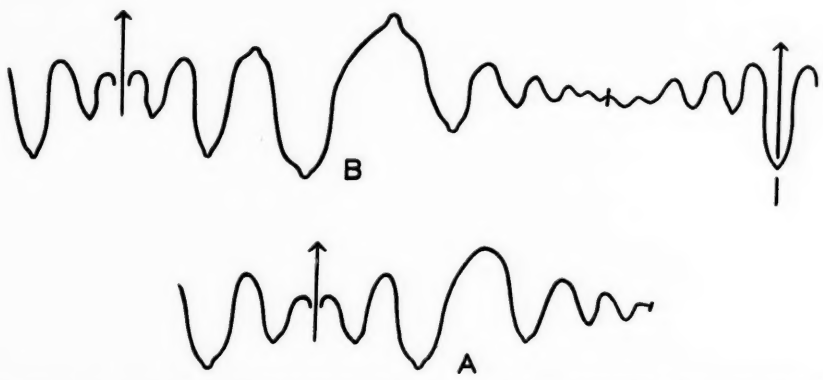
The name refers to the evolutionary intermediate position of this genus between *Eobeloceras* and *Beloceras*.

Affinities.—*Mesobeloceras* is known from two similar species, one from the Fitzroy Basin of Western Australia, described below as *Mesobeloceras thomasi*, and the other an undescribed species from Morocco (see Pl. 4, fig. 1 of this report). *Eobeloceras* Schindewolf (1936) is not well known as regards cross section and internal suture, but from the available information it is clear that *Mesobeloceras* lies intermediate along the evolutionary line from this genus to *Beloceras* Hyatt (1884). In fact, so obvious are the affinities between the three genera that it is to be expected that future discoveries of Frasnian ammonoids will establish a series of morphologically intermediate forms which are transitional between the generic stages. The form of the suture at once establishes the close relationships between the genera, and enables them to be readily separated. All three have the characteristic beloceratid shape to the sutural elements, but whereas *Eobeloceras* has a primary ventral lobe divided into only two pairs of adventitious lobes, *Mesobeloceras* has three pairs of adventitious lobes, and *Beloceras* has as many as seven pairs in mature specimens. Similarly, *Eobeloceras* has up to three pairs of lobes between the first lateral saddle and the line of involution, whereas *Mesobeloceras* has up to five pairs, and *Beloceras* as many as eight pairs. The whorl cross section of *Eobeloceras* is imperfectly known, but again an evolutionary trend is apparent, from the evolute *Eobeloceras* through *Mesobeloceras* to the moderately involute form of *Beloceras* with its comparatively small umbilicus and flat compressed whorls.

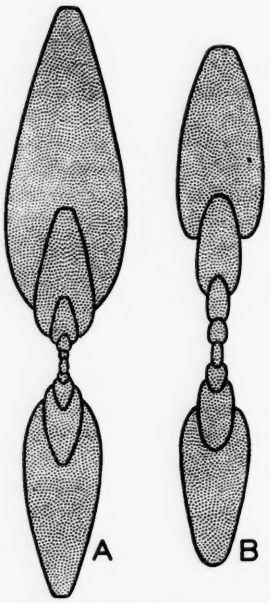
An imperfectly known species. *Beloceras acutodorsatum* Dybczński (1913, p. 521–522), from the Upper Devonian of Poland, may eventually be proved to belong in *Mesobeloceras*. Dybczński shows the external suture to consist of eight pairs of lobes, the same number as in mature specimens of *Mesobeloceras thomasi*, but half of his sutural drawing consists of broken lines. Moreover, he shows the venter to be acutely angular, although this may be, in part, a function of weathering. Finally, the flanks are traversed by broad ribs. Dybczński's description and illustrations indicate that *Beloceras acutodorsatum* is more closely comparable to *Mesobeloceras thomasi* than to any other described species. However, it is questionable whether the two species are congeneric.

MESOBELOCERAS THOMASI Glenister, n. sp.
Pl. 8, fig. 2; Pl. 10, fig. 6; Text-figs. 12A,B,13B

Description.—This species is known from twelve well-preserved specimens, half of them being fragmentary. The largest individual has a maximum over-all shell diameter of 85 mm., but most of the representa-



TEXT-FIG. *12*—Diagrammatic representations of the suture of *Mesobeloceras thomasi* Glenister, n. sp. A, paratype 1745, ×9, at a diameter of 16 mm.; B, composite drawing, external suture from holotype 1742, ×5, at a diameter of 35 mm., internal suture from paratype 1743, at approximately the same diameter.



TEXT-FIG. *13*—Diagrammatic representations of cross sections of *Beloceras* and *Mesobeloceras*. A, *Beloceras sagittarium* (G. & F. Sandberger), figured specimen 1749, slightly more than ×1; B, *Mesobeloceras thomasi* Glenister, n. sp., paratype 1744, ×2.

tives are about half of this size. The conch is strongly compressed laterally and is thus thinly discoidal. Mature whorls have a flat narrow venter, have flattened ventrolateral flanks, and are evenly rounded across the dorsolateral area. They are shallowly impressed dorsally, so that the shell is evolute. Earlier-formed volutions are more uniformly rounded and do not develop either the flattened ventrolateral flanks or the flat venter; they are proportionally less impressed dorsally than mature volutions. The siphuncle is marginal and ventral in all observed growth stages.

The early whorls are extremely narrow, and are rarely preserved. However, mature specimens appear to develop from four to five whorls, slightly more than half a volution being represented by living chamber. The septa are closely crowded, 50 being present in the final whorl of a specimen of 36 mm. maximum over-all shell diameter. Growth lines are present on well preserved specimens. They are directed radially from the line of involution across the dorsolateral flanks, turn sharply orad to form a prominent ventrolateral salient, and then swing sharply apicad to produce a deep but narrow sinus across the flattened venter. A runzelschicht is prominently developed.

The complexity of the suture varies within wide limits, depending on the growth stage attained. Mature sutures consist of as many as twelve pairs of lobes and a dorsal lobe. The primary ventral lobe of mature specimens is divided into three pairs of adventitious lobes, the third pair generally being added at an over-all shell diameter of approximately 17 mm. The first lateral saddle is followed by a maximum of nine pairs of lobes and a deep narrow dorsal lobe. Both saddles and lobes are strikingly similar in outline to those of *Beloceras*.

This species is named in grateful recognition of the work of Mr. G. A. Thomas, of the Commonwealth of Australia Bureau of Mineral Resources, who collected many of the specimens under study and supplied the author with a considerable amount of stratigraphic information.

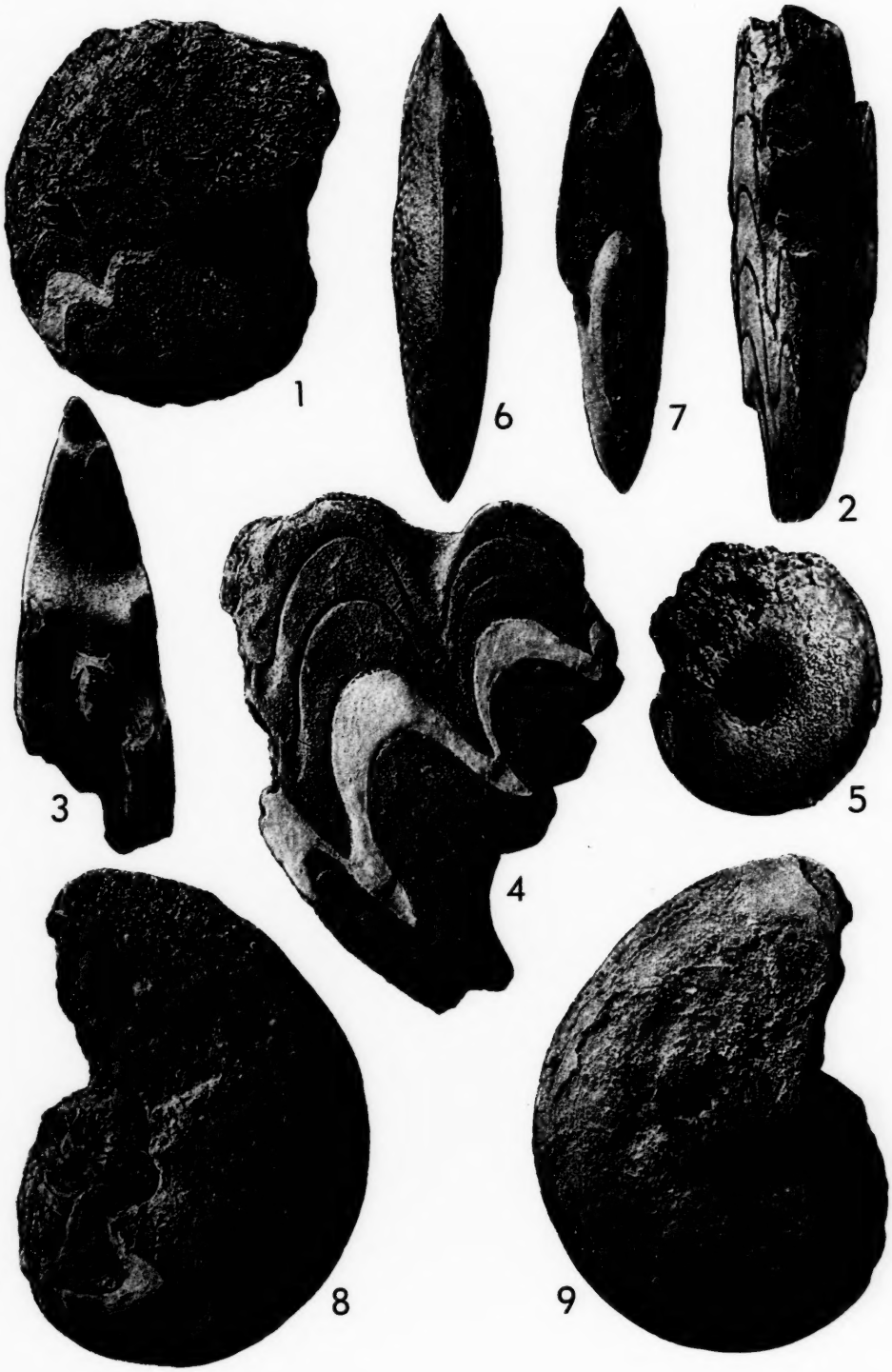
Occurrence.—All specimens came from the Fossil Downs Formation, 4–6 feet above a massive limestone, assumed by field parties to be the Pillara Limestone. They are associated with *Beloceras sagittarium* and *Manticoceras guppyi*, and are thus clearly of the same age as the Oberdevonstufe I $(\beta)\gamma$. K Du 479.

Repository.—Holotype 1742 and paratypes 1743–1745 are lodged with the Commonwealth of Australia Bureau of Mineral Resources in Canberra.

Comparisons.—The relationship of *Meso-*

EXPLANATION OF PLATE 11

FIG. *1–5*—*Timanites angustus* Glenister, n. sp.; *1*, paratype 1739, ×1½; *2–4*, holotype 1737, ×2; *5*, paratype 1740, ×8. See also Pl. 12, fig. 9, Text-fig. 9.
6–9—*Neomanticoceras erraticum* Glenister, n. sp., holotype 1714, ×1½. See also Text-figs. 10A,11.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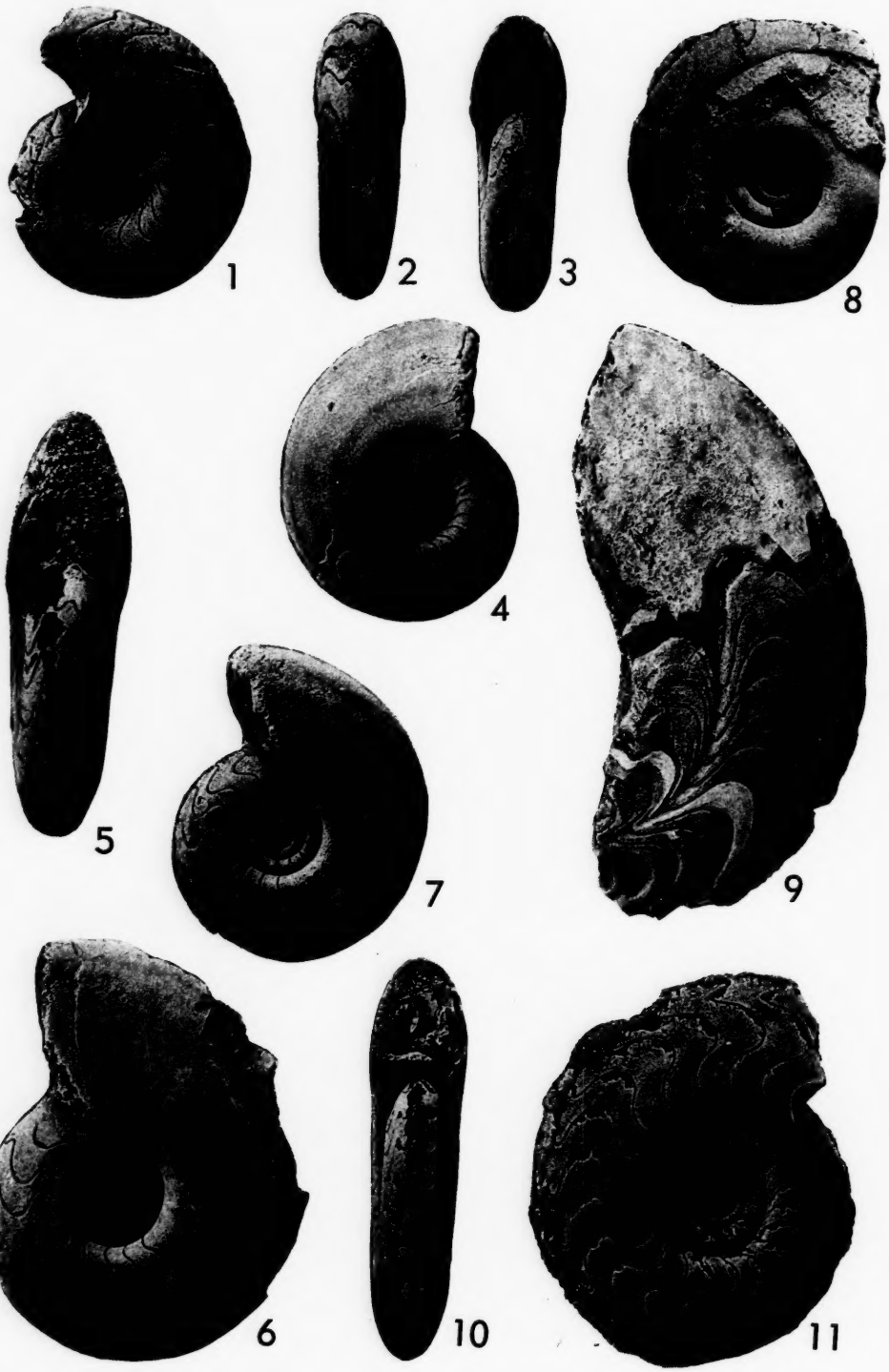
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beloceras thomasi to species of *Eobeloceras* and *Beloceras* has been considered under the generic diagnosis. The only congeneric form known to the author is from Erfoud, and is at present lodged in the Morocco-Clariond Collection of the State University of Iowa (No. 9635; see Pl. 4, fig. 1 of this report). The Moroccan specimen belongs to a new species, which is readily separated from *Mesobeloceras thomasi* by the more primitive suture of the former. Although fragmentary, the African specimen indicates that the third pair of adventitious lobes is not developed until the phragmocone has attained a maximum over-all shell diameter of approximately 90 mm. At this diameter only four pairs of lobes appear in the external suture between the first lateral saddle and the line of involution.

Genus BELOCERAS Hyatt, 1884

Type species.—*Goniatites sagittarius* G. & F. Sandberger, 1851.

In establishing the genus *Beloceras*, Hyatt (1884, p. 333) referred to it "only one species but the most remarkable and in many characteristics the most instructive of Devonian forms," *Ammonites multilobatus* Beyrich. However, it later became apparent that *A. multilobatus* Beyrich is a junior homonym of *A. multilobatus* Bronn (1832, p. 159–160). It is difficult to determine when a valid name was first given to the group of *A. multilobatus* Beyrich. Specimens showing close similarities in external morphology to this specific group were described by d'Archiac & de Verneuil (1842) under the new name of *Goniatites tenuistriatus*. The details of surface ornamentation, cross section and coiling of this species strongly suggest it is synonymous with *Ammonites multilobatus*. However, the sutures have never been illustrated, and they cannot be determined from the authors' description; without a knowledge of them it is impossible to assign *Goniatites tenuistriatus* to a restricted genus. There is general agreement that *Goniatites sagittarius* G. & F. Sandberger (1851) is conspecific with *Ammonites multilobatus*, and the former is generally accepted as the type of *Beloceras*. However, it must not be forgotten that future work on the type material of *Goniatites tenuistriatus* might well prove it to possess a suture similar to that of *Ammonites multilobatus* Beyrich. In that event, *Goniatites tenuistriatus* would become the type species of *Beloceras*.

Wherever the exact stratigraphic occurrence of this genus is known, it is found to be restricted to the *Manticoceras*-Stufe I (β)γ and Iδ or its equivalents.

BELOCERAS SAGITTARIUM (G. & F. Sandberger), 1851

Pl. 5, fig. 12; Pl. 10, fig. 7; Pl. 13, figs. 1–5; Pl. 14, figs. 1–8; Text-figs. 13A,14,15A–E

1837. *Ammonites multilobatus* Beyrich, Beiträge Kenntn. Verstein. rhein. Übergangsgeb., p. 33–34, pl. 1, fig. 9. [Not *Ammonites multilobatus* Bronn, 1832.]

(?)1842. *Goniatites tenuistriatus* d'Archiac & de Verneuil, Geol. Soc. London, Trans., ser. 2, v. 6, p. 343, pl. 26, figs. 7,7a,7b,8,8a.

1842. *Goniatites multilobatus* d'Archiac & de Verneuil, *ibid.*, p. 383.

1848. *Goniatites multilobatus* Bronn, Gesch. d. Natur, v. 3, p. 543.

1850. *Aganides multilobatus* d'Orbigny, Prod. de Paléont. Stratigr., v. 1, p. 59.

1850. *Aganides tenuistriatus* d'Orbigny, *ibid.*, v. 1, p. 61.

1851. *Goniatites sagittarius* [part] G. & F. Sandberger, Verstein. rhein. Schichtensyst. Nassau, p. 77–81, pl. 4, figs. 3,3a–i,3l; p. 56, fig. 7. [Not pl. 4, fig. 3k.]

1852. *Ammonites multilobatus* Giebel, Fauna der Vorwelt, v. 3, p. 493.

1873. *Pinacoceras multilobatum* Mojsisovics, Ab-

EXPLANATION OF PLATE 12

FIG. *1–4*—*Ponticeras* cf. *P. aequabile* (Beyrich); State University of Iowa figured specimens 9634, from the *Manticoceras* Zone 15 km. east of Taouz, Morocco, ×2; figs. *1–3* are views of the one specimen.

5–8—*Hoeninghausia pons* Glenister, n. sp.; *5,6*, holotype 35767, ×4; *7*, paratype 35768, ×4; *8*, paratype 35769, ×4. See also Pl. 5, figs. 4–6, Text-figs. 8A–D.

9—*Timanites angustus* Glenister, n. sp., paratype 1738, ×1½. See also Pl. 11, figs. 1–5, Text-fig. 9.

10,11—*Ponticeras discoidale* Glenister, n. sp., holotype 1720, ×2. See also Pl. 5, figs. 7–9, Text-figs. 1C,2A.

handl. k.-k. geol. Reichsanst. Wien, v. 6, p. 43,69.

1879. *Goniatites multilobatus* Roemer, Zeitschr. dtsch. geol. Ges., v. 31, p. 660.

1880. *Goniatites multilobatus* Roemer, Geol. Mag., new ser., dec. 2, v. 7, p. 145–7, pl. 5, figs. 1,2.

1881. *Goniatites multilobatus* Branco, Palaeontographica, v. 27, p. 22,23,33, pl. 6, figs. 6a–d.

1882. *Goniatites multilobatus* Holzapfel, Palaeontographica, v. 28, p. 237, pl. 45 (ii), figs. 2, 2a,3,4,4a,5,5a,6,6a,6b.

1884. *Beloceras multilobatum* Hyatt, Boston Soc. Nat. Hist., Proc., v. 22, p. 333–334.

1884. *Goniatites* (*Beloceras*) *multilobatus* Zittel, Handb. Palaeontol., v. 2, p. 415, 421, figs. 562,581.

1887. *Goniatites* (*Beloceras*) *multilobatus* Frech, Z. dtsch. geol. Ges., v. 39, p. 389,428,432.

1889. *Goniatites multilobatus* Kayser, Neues Jb., v. 1, p. 184.

1890. *Beloceras multilobatum* Steinmann and Döderlein, Elem. d. Paläont., p. 396, fig. 476.

1890. *Goniatites sagittarius* Ussher, Quart. Jour. Geol. Soc. London, v. 46, p. 509–511.

1896. *Goniatites* (*Beloceras*) *multilobatus* Peetz, Travaux Sect. Géol. Cabinet Majesté, St. Pétersbourg, v. 1, livr. 3, p. 174,197.

1897. *Beloceras sagittarium* Foord and Crick, Cat. Fossil Ceph., pt. 3, p. 273–276, fig. 133.

1901. *Beloceras multilobatum* Drevermann, Preuss, geol. Landesanstalt Berlin, Jahrb. f. 1900, p. 122.

1902. *Beloceras multilobatum* Frech, Beitr. Paläont. u. Geol. Oesterreich-Ungarns u. Orients, v. 14, p. 61.

1913. *Beloceras multilobatum* Frech, Fossilium Catalogus, v. 1, Animalia, pars 1, p. 26.

1913. *Beloceras multilobatum* Wedekind, Gesell. Naturforschender Freunde Berlin, S.-B., Jahrg. 1913, p. 29–30, 44–49, figs. 4,5.

1918. *Beloceras multilobatum* Wedekind, Palaeontographica, v. 62, p. 129–130, pl. 21, fig. 13.

1921. *Beloceras multilobatum* Schindewolf, Z. dtsch. geol. Ges., v. 73, p. 172,197.

1931. *Beloceras multilobatum* Matern, Preuss. geol. Landesanstalt Berlin, Abh. Neue Folge, Heft 134, p. 76–77.

1935. *Beloceras multilobatum* Böhm, Études sur les faunes du Dévonian Supérieur et du Carbonifère Inférieur de la Montagne Noire, p. 51–53, pl. 1, figs. 4a,b,5.

1938. *Ammonites multilobatus* Miller, Geol. Soc. Am., Spec. Pap. 14, p. 132–134.

1938. *Beloceras sagittarium* Miller, *ibid.*

1938. *Beloceras multilobatum* Wade, Australian and New Zealand Assoc. Adv. Sci., v. 23, (Auckland Meeting), p. 93–96.

1941. *Beloceras multilobatum* Teichert, Am. Jour. Sci., v. 239, p. 149–150.

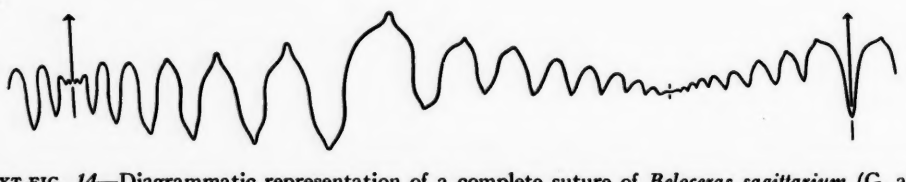
1943. *Beloceras sagittarium* Teichert, Am. Jour. Sci., v. 241, p. 86.

1949. *Beloceras sagittarium* Teichert, Comm. Australia, Bur. Min. Res., Rept. 2, p. 18.

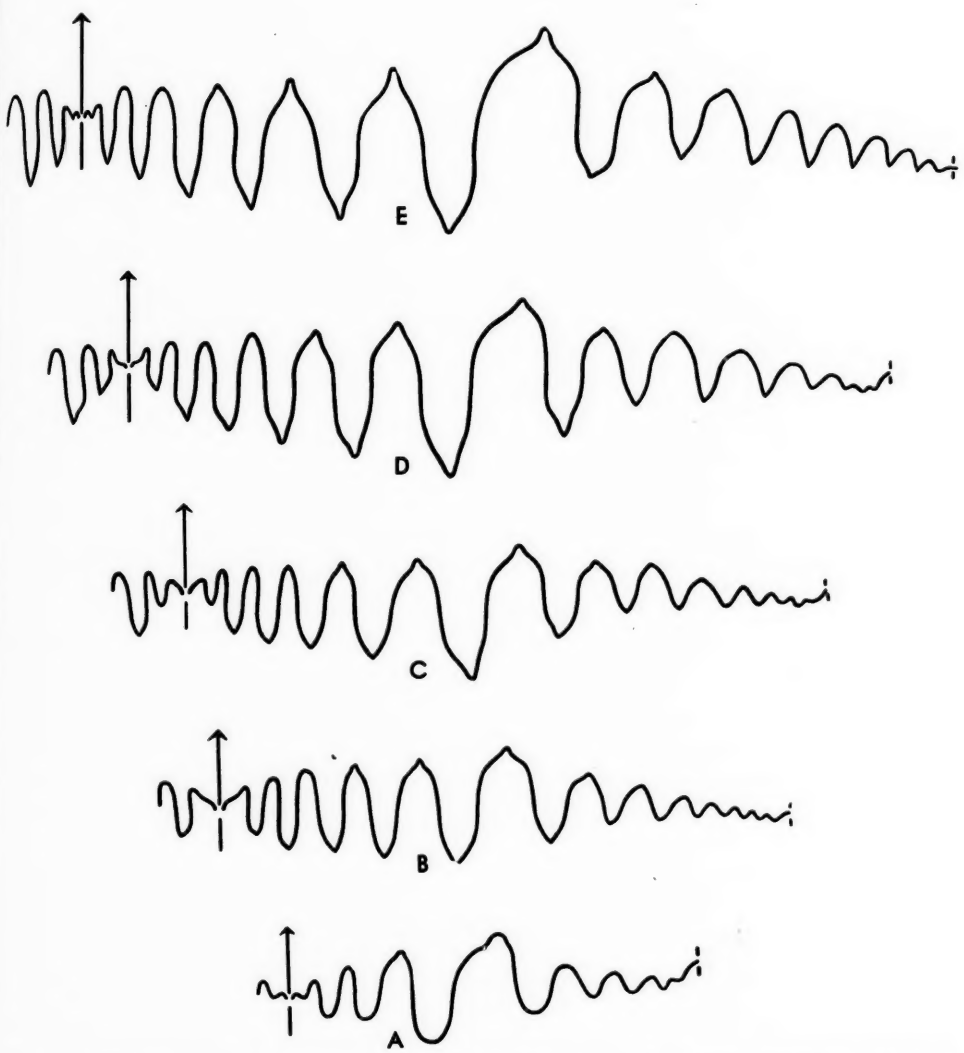
1950. *Beloceras sagittarium* H. and G. Termier, Paléont. Maroc., v. 2, p. 54, pl. 150, figs. 50–51; pl. 151, figs. 25–27.

In 1851 G. & F. Sandberger first adequately described and gave a valid name to this unique species of Upper Devonian ammonoids. Since this date, *Beloceras sagittarium* has become one of the better known ammonoid species. It occurs commonly in Germany, has been described from France, and is probably also to be found in England, Russia, and North Africa. Its presence in Australia was first indicated by Wade (1938) and later considered by Teichert (1941, 1943, 1949). However, the following is the first detailed description of the Australian representatives; it is based solely on Australian specimens.

Description.—The conch is greatly compressed laterally, and develops an almost lenticular cross section. Each whorl has a narrow but flat venter, has flattened ventrolateral flanks, and has gently rounded umbilical shoulders. It is deeply impressed dorsally, so that the shell is moderately involute and the umbilicus is narrow. Only in the later growth stages does the umbilical diameter exceed one-fifth that of the corresponding over-all shell diameter. The siphuncle is ventrally situated and marginal in even the smallest observed whorl.



TEXT-FIG. *14*—Diagrammatic representation of a complete suture of *Beloceras sagittarium* (G. and F. Sandberger), ×1½. External suture based on figured specimen 35773, at a diameter of 126 mm.; internal suture based on figured specimen 1750 at about the same stage of ontogenetic development.



TEXT-FIG. *15*—Diagrammatic representations of external sutures of *Beloceras sagittarium* (G. and F. Sandberger), during ontogenetic development. A, figured specimen 1748, ×9, at a diameter of 14 mm.; B, figured specimen 1751, ×4, at a diameter of 36 mm.; C, figured specimen 1761, ×3¾, at a diameter of 48 mm.; D, figured specimen 1746, ×3½, at a diameter of 50 mm.; E, figured specimen 35773, ×2, at a diameter of 126 mm.

The involute nature of the conch and the secretion of a thin ribbon of shell material in the vicinity of the umbilical seam make it difficult to determine the number of whorls present, especially in mature forms. Specimen 1748 consists of four whorls when its diameter is 20 mm. However, mature whorls expand rapidly in diameter, and it seems unlikely that even the largest of the Australian specimens develops more than seven whorls. The largest known specimen from the Fitzroy Basin has a maximum diameter of 126 mm., but it is septate throughout. Remnants of the callus along the umbilical seam show that at least one-third of a whorl has been broken away. Other mature speci-

mens have an average of slightly more than one-half of a volution represented by body chamber. Assuming that the adoral end of the large specimen represents the base of the living chamber, and that only a further half volution was developed, it is estimated that maximum over-all diameter of the complete shell would have been at least 230 mm. Slightly more than 60 septa per whorl occur in the mature volutions of the larger specimens. A large bulbous protoconch projects above the general level of the umbilical floor in well preserved specimens. Slight weathering results in the destruction of the protoconch, thereby making the umbilicus appear to be perforate.

The growth striations are delicate, and are thus only preserved on a few specimens. They are convex, traversing the dorsolateral and lateral areas radially, and turning adapically across the ventrolateral area to form a deep but narrow ventral sinus. On nearing the venter, some of the growth lines become elevated to form lirae. These are evenly spaced, 40 such lirations being present in half a volution of a shell of 25 mm. maximum over-all diameter. None of the specimens in the author's collection exhibits a complete mature aperture. The runzelschicht or wrinkle layer, reported from many ammonoids and some few nautiloids (Teichert & Glenister, 1952, p. 749), is well preserved on several of the specimens. Although the wrinkles are somewhat irregular in orientation, they are generally transverse with slight adoral convexity. However, they become complexly bunched and trend sharply adapically just ventrad of the line of involution.

The suture line varies in complexity, within wide limits, depending on the growth stage. Mature sutures consist of as many as 25 pairs of lobes, together with the deep dorsal lobe and the shallow azygous secondary ventral lobe. Sutural elements are added across the line of involution, and also on either side of the secondary ventral lobe. Eight lobes are developed, at an early growth stage, between the first lateral saddle and the line of involution. These sutural elements change their shape during ontogenetic development, but the number present remains almost constant. The number of adventitious lobes increases steadily with ontogeny, so that at maturity they may be only slightly fewer than the auxiliary lobes.

Occurrence.—*Beloceras sagittarium* is locally abundant in some of the impure limestones of the Fitzroy Basin. Most of the known specimens are from the Virgin Hills Formation, although a few were collected from the Fossil Downs Formation. One hundred forty specimens are represented in the author's collections, many of them being well preserved and virtually complete. C 17 (figured specimen 35773), RS 190 (all other figured specimens except 1752), K Du 479 (figured specimen 1752), RS 142, RS 181, RS 190 A–C, R 304, R 312, R 315, B 78, C 10, C 12–13, C 27–32, K Dud 149, K Dup 152, K Dup 155. The species is associated with *Ponticeras retorquatum*, *Manticoceras guppyi*, *M. cinctum*, *Neomanticoceras erraticum*, *Mesobeloceras thomasi*, and *Tornoceras* (*Tornoceras*) *clausum*.

Repository.—Specimen 35773 is lodged in the Department of Geology of the University of Western Australia, in Perth, and the remaining figured specimens, numbered 1746–1752, and 1761, are deposited with the Commonwealth of Australia Bureau of Mineral Resources in Canberra.

Comparisons.—Several of the described species of *Beloceras* are known from numerous specimens and have been recorded from widely separated localities. The genus is also known from a large quantity of well preserved material from Western Australia. The detailed comparison of the Australian specimens with those of other known species of *Beloceras* is thus of considerable interest.

Although the Australian material clearly

EXPLANATION OF PLATE 13

FIG. *1–5*—*Beloceras sagittarium* (G. & F. Sandberger); *1,3*, figured specimen 1747, ×2; *2*, figured specimen 1750, ×1½ (external suture shown on the adoral portion of the specimen, and internal suture of the succeeding whorl on the adapical half); *4,5*, figured specimen 35773, ×1. See also Pl. 5, fig. 12, Pl. 10, fig. 7, Pl. 14, figs. 1–8, Text-figs. 13A,14,15A–E.

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belongs in the same generic group as *Beloceras praecursor* Frech (1902), *Goniatites kayseri* Holzapfel (1882), and *Beloceras denckmanni* Wedekind (1913), it is specifically distinct from these forms. *Beloceras praecursor* is readily distinguished by its suture, *Goniatites kayseri* is a more evolute form, and *Beloceras denckmanni* is much broader in whorl cross section. However, examination of numerous published descriptions and illustrations, and study of a specimen from the Martenberg Klippe, near Adorf, have shown that the Australian forms are closely similar to the European representatives of *Beloceras sagittarium* (G. & F. Sandberger, 1851). Consistent differences between the Australian and the European specimens do occur, but they are slight, and are not considered by the present author to be of sufficient importance to warrant the erection of a new species. The most consistent difference between the two groups is that the growth lines of the Australian forms are convex, whereas those of the European group are generally weakly biconvex. The degree of convexity seems to vary slightly in both the Australian and the European forms, and complete gradation will probably be demonstrated in future collections. A ventrolateral flattening of the flanks is characteristic of the European specimens referred to *Beloceras sagittarium*, and many forms are gently concave in this area. Australian specimens apparently do not develop this concave zone, although a flattening in the curvature of the ventrolateral flanks is common. The flatly bicarinate venter, which has been recorded (Wedekind, 1913, p. 48) in the early growth stages of European forms, is replaced by a narrow flat ventral zone in Australian specimens.

Some paleontologists may criticize the present author for "lumping" this Australian material into a European species. The Kimberley specimens show a striking similarity to the type material of *Beloceras sagittarium*. It is felt that the erection of a new species would place too much accent on insignificant differences, whereas the placement of the specimens within the European species draws attention to the remarkable uniformity of the group.

Suborder GONIATITINA Hyatt, 1884

[*ex* Goniatitinae]

Superfamily CHEILOCERATACEAE Frech, 1897

[*ex* Cheiloceratidae]

Family TORNOCERATIDAE Arthaber, 1911

[*ex* Tornoceratea]

The family Tornoceratidae, as interpreted by the present author, includes the following genera: *Tornoceras* Hyatt (1884), *Pseudoclymenia* Frech (1897), *Lobotornoceras* Schindewolf (1936), and *Posttornoceras* Wedekind (1910). Its time range is from Middle to Upper Devonian.

Genus TORNOCERAS Hyatt, 1884

Type species.—Goniatites uniangularis Conrad, 1842.

Miller (1938, p. 140–144) has given an excellent outline of the taxonomy and legal status of *Tornoceras* and its subgenera. The present author is in total agreement with the opinions expressed in this work, and recognizes the following subgenera of *Tornoceras* (largely after Miller).

Tornoceras s.s. Hyatt (1884, p. 320–321); type species, *Goniatites uniangularis* Conrad (1842, p. 268). Umbilicus closed (or nearly so); ventrolateral zones of conch rounded and not marked by longitudinal grooves; sutures form high, prominent saddles on ventrolateral zones of conch.

Parodoceras ["*Parodiceras*"] Hyatt (1884, p. 319–320); type species, *Goniatites discoideus* Hall (1860, p. 97–98). Umbilicus closed; ventrolateral zones of conch rounded

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EXPLANATION OF PLATE 14

FIG. *1–8—Beloceras sagittarium* (G. & F. Sandberger); *1–3*, figured specimen 1751, ×2; *4,5*, figured specimen 1748, ×2; *6–8*, figured specimen 1746, ×1. See also Pl. 5, fig. 12, Pl. 10, fig. 7, Pl. 13, figs. 1–5, Text-figs. 13A,14,15A–E.

and not marked by longitudinal grooves; sutures form very low, scarcely recognizable saddles on ventrolateral zones of conch.

Protornoceras [non *Pernoceras*] Dybczński (1913, p. 512–517); type species, *Protornoceras polonicum* Dybczński (1913, p. 515–516). Umbilicus open and infundibuliform; ventrolateral zones of conch rounded and not marked by longitudinal grooves; sutures form prominent saddles on ventrolateral zones of conch.

Aulotornoceras Schindewolf (1922, p. 188–189); type species *Goniatites auris* Quenstedt (1846, p. 64). Umbilicus variable, closed or open and infundibuliform; ventrolateral zones of conch marked by longitudinal grooves; sutures form high, prominent saddles on ventrolateral zones of conch.

Polonoceras Dybczński (1913, p. 519–520); type species, *Polonoceras planum* Dybczński (1913, p. 520). Umbilicus closed; ventrolateral zones of conch angular and not marked by longitudinal grooves; sutures form high prominent saddles on ventrolateral zones of conch.

Additional consideration of the subgenus *Polonoceras* is warranted. It was originally designated, with full generic rank, to include two then new species, *Polonoceras latum* and *Polonoceras planum* Dybczński (1913), from the Upper Devonian of Poland. Miller (1938, p. 142) reduced the taxon to subgeneric rank, designating *Tornoceras* (*Polonoceras*) *planum* as the subgenotype, and correctly referred *P. latum* to *Protornoceras*. The accuracy of Dybczński's representation of the suture line of *Polonoceras planum* (1913, Tablica 1, p. 524; see Text-fig. 17C of the present report) must be questioned. His unretouched plate gives no indication of the singularly unusual angularity of the saddles which he shows in the suture drawing; such sutural contours, if accurately represented, have no known equivalents. However, it seems likely that Dybczński's drawings are somewhat inaccurate. The plates suggest that the suture of *Polonoceras planum* is similar to that of the species described below as *Tornoceras* (*Polonoceras*) n. sp. In addition, the cross section and shell form of the two species are comparable, so that they should probably be placed together in the one subgenus. No other species of *Polonoceras* have been recorded.

TORNOCERAS (TORNOCERAS) CONTRACTUM Glenister, n. sp.

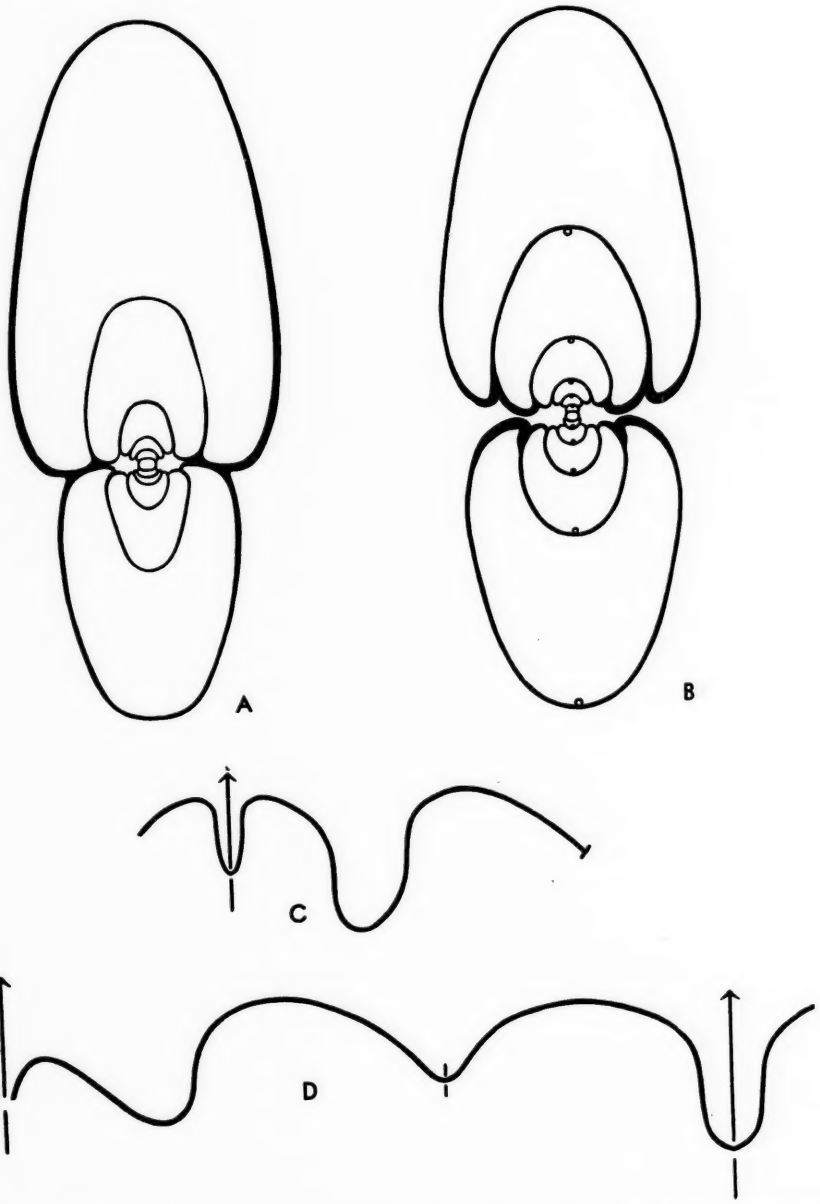
Pl. 15, figs. 4–6; Text-figs. 16B,D

Description.—This species is represented in the author's collections by the type material and some fifty additional specimens. The outer shell is missing from all of the known representatives, but otherwise they are in an excellent state of preservation. The largest specimen known to the author has a maximum over-all shell diameter of 54 mm., but most of the forms, including the holotype, are only approximately half this size. Immature whorls are uniformly rounded across the flanks and venter. As maturity is approached, the flanks become flattened, although they remain gently convex in even the largest specimens. The conch is evolute and widely umbilicate in the early growth stages, but at maturity it becomes narrowly umbilicate and almost completely involute. The narrowing of the umbilicus is partly due to a conspicuous thickening of the shell in this area. However, the umbilicus remains open in all observed growth stages. The siphuncle is in contact with the shell wall as far apicad as the first-formed volution.

The paratype has five whorls, but it is likely that larger specimens develop as many as seven. One of the larger individuals retains a portion of the aperture, and shows that three-quarters of the ultimate whorl consists of body chamber. The aperture is probably biconvex, but only the deep rounded ventral sinus and the prominent ventrolateral salient have been observed.

At maturity, the complete suture consists of six lobes and intervening saddles. The secondary ventral lobe is small and V-shaped, and is succeeded, in turn, by the low rounded ventrolateral saddle, a broad asymmetric adventitious lobe, a broadly rounded dorsolateral saddle, and a symmetrical first lateral lobe. The latter is centered on the line of involution, and it is separated from the unusually deep linguloid dorsal lobe by a flatly rounded saddle. Nineteen septa occur in the ultimate volution of the holotype (27.5 mm. maximum over-all shell diameter).

The trivial name is derived from the Latin for "contracted" and refers to the decrease



TEXT-FIG. *16*—Diagrammatic representations of cross sections and sutures of *Tornoceras* (*Tornoceras*) *clausum*, and *Tornoceras* (*Tornoceras*) *contractum* Glenister, n. spp. (line thickness in cross sections accurately reflects thickness of shell). A, *Tornoceras clausum*, paratype 1757, ×3; B, *Tornoceras contractum*, paratype 1755; ×4; C, *Tornoceras clausum*, holotype 1756, ×3½, at a diameter of approximately 23 mm.; D, *Tornoceras contractum*, holotype 1753, ×3½, at a diameter of 27 mm.

in the diameter of the umbilicus as maturity is approached.

Occurrence.—K Dup A 95. The species is found in the Gogo Formation in association with specimens of *Timanites angustus*. It is thus of the age of the *Manticoceras*-Stufe Iα.

Repository.—Holotype 1753 and paratypes 1754–1755 are lodged with the Commonwealth of Australia Bureau of Mineral Resources in Canberra.

Comparisons.—This species clearly belongs in *Tornoceras* sensu stricto, and lies close to the type species of the genus, *Tornoceras* (*Tornoceras*) *uniangulare* (Conrad). The Western Australian species is distinct in lacking the bulbous expansion at the adapical end of the dorsal lobe and in the maintenance of an open umbilicus during all growth stages.

TORNOCERAS (TORNOCERAS) CLAUSUM Glenister, n. sp.

Pl. 15, figs. 7–9; Text-figs. 16A,C

Description.—The holotype, one paratype, and six additional specimens of this species are available for study. All specimens are well preserved, although slightly worn externally. The holotype is the largest form known, having a maximum over-all shell diameter of 41 mm., whereas the smallest specimen measures 18 mm. in diameter. At maturity the whorls are compressed laterally, although they are still slightly convex, whereas the venter and the dorsolateral flanks are uniformly rounded. Early-formed whorls are more uniformly rounded, and they lack the flattening of the flanks. The shell is evolute and widely umbilicate during early growth stages. However, the umbilicus reaches its maximum diameter at about the third whorl, and it then becomes reduced in caliber so that it is closed in the fourth volution; mature forms are completely involute. The shell is conspicuously thickened in the vicinity of the umbilicus, but there is evidence, still inconclusive, of the presence of a small umbilical callus similar to that described for *Nautilus* (see Miller, 1947, p. 16–17).

A maximum of five whorls is known to be formed in this species, the body chamber occupying slightly more than three-quarters of a whorl. A runzelschicht is prominently developed; the wrinkles are unusually irregular in orientation, and they tend to display concentric rather than transverse patterns. Numerous fine lirations traverse the shell; they are weakly developed on the flanks, but become more pronounced ventrally. A deep rounded lobe forms across the venter, and it is followed by a prominent salient across the ventrolateral area, a shallow broadly rounded lobe across the flanks, and a less conspicuous dorsolateral saddle. The aperture is partially preserved in the holotype. It apparently parallels the course of the lirations.

At maturity each complete external suture consists of three lobes and intervening saddles. The deep azygous secondary ventral lobe is flanked in turn, by a high asymmetric ventrolateral saddle, a large asymmetric lobe across the flanks, and a broad rounded dorsolateral saddle. The prominent sutural element across the flanks is really an adventitious lobe, for ontogenetic studies of *Tornoceras* have shown that the pair of lobes, which at maturity are located on the umbilical portions of the conch, are formed immediately after the azygous secondary ventral and dorsal lobes, and are thus the first lateral lobes.

The name is derived from the Latin, and it refers to the closure of the umbilicus at maturity.

Occurrence.—RS 190 (all types), RS 190 A, R 304, K Dud 149. It is found in the Virgin Hills Formation, associated with *Beloceras sagittarium*, *Ponticeras retorquatum* and *Manticoceras guppyi*, and is thus of the age of the *Manticoceras*-Stufe I (β)γ.

Repository.—Holotype 1756 and paratype 1757 are lodged with the Commonwealth of Australia Bureau of Mineral Resources in Canberra.

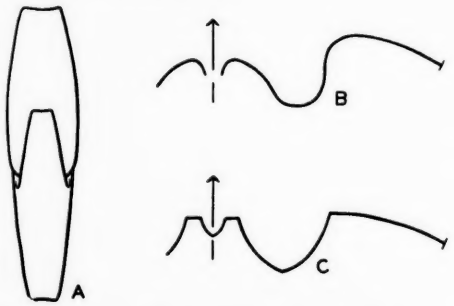
Comparisons.—The deep secondary ventral and adventitious lobes (the latter across the flanks) of this species, together with the closed umbilicus, serve to separate it from *Tornoceras contractum* Glenister, n. sp., which occurs in the underlying *Manticoceras*-Stufe Iα equivalents of the same general Fitzroy Basin locality. *Tornoceras clausum* falls within *Tornoceras*, sensu stricto, and is generally similar to the type species of this genus, *Tornoceras* (*Tornoceras*) *uniangulare* (Conrad). However, it differs from this and all similar species in the combination of closed umbilicus and a high saddle separat-

ing the deep secondary ventral and adventitious lobes.

TORNOCERAS (POLONOCERAS) sp.
Pl. 15, fig. 1; Text-figs. 17A,B

Description.—This species is known from two specimens, each of which is slightly worn. The larger has a maximum over-all shell diameter of 16 mm., and is probably almost complete. The conch is flatly discoidal and narrowly umbilicate. It should be noted that the figured specimen (Pl. 15, fig. 1) is weathered around the umbilical region, so that the umbilicus assumes at least double its original diameter. The whorls are strongly compressed and flattened across the flanks. Angular ventrolateral shoulders bound a shallowly concave venter. The umbilical shoulders are not preserved in the outer whorls of either specimen, but they are almost certainly narrowly curved; the whorls are impressed dorsally to a moderate depth. Slightly more than half a whorl is represented by body chamber in both specimens. The siphuncle is relatively large, and it is marginal in all observed growth stages.

The external suture consists of a total of three saddles and intervening lobes. The azygous secondary ventral lobe is flanked, in turn, by a pair of low asymmetric saddles across the ventrolateral area, a deep rounded (adventitious) lobe across the flanks, and a broadly rounded asymmetric saddle across the dorsolateral area.



TEXT-FIG. *17*—Diagrammatic representations of sutures and cross section of *Tornoceras* (*Polonoceras*) sp., and *Tornoceras* (*Polonoceras*) *planum* Dybczński. A,B, *Tornoceras* sp., figured specimen 1758, A, ×2½, B, ×5, at a diameter of 9 mm.; C, *Tornoceras planum* (after Dybczński), probably ×7, and at a diameter of approximately 9 mm.

The poor preservation and small number of available specimens render it unwise for the present author to elect a trivial name for this species.

Occurrence.—K Dul 478. Fossil Downs Formation.

Repository.—Figured specimen 1758 is lodged with the Commonwealth of Australia Bureau of Mineral Resources in Canberra.

Comparisons.—The flattened venter, and the angular ventrolateral shoulders place this species in *Polonoceras*. Unfortunately, the type species of this subgenus is imperfectly known, for Dybczński's illustrations are poor and his drawings are of questionable accuracy. Thus, although the Fitzroy Basin species undoubtedly belongs in *Polonoceras*, detailed comparisons between it and the type species of the subgenus cannot yet be made.

LOCALITIES

(1) *Joint collection of Commonwealth of Australia Bureau of Mineral Resources and West Australian Petroleum Pty., Limited*

K Du 479—Horse Spring Range, in the vicinity of Horse Spring—126° 02′ E, 18° 12′ S—Fossil Downs Formation, 4–6′ above base.

K Dud 149—SE end of Bugle Gap, 3¼ miles at 61° from Pinnacle Spring—126° 05′ E, 18° 44½′ S—Virgin Hills Formation, flanking and overlying a bioherm of the Pillara Formation.

K Dud 271—Pillara Range, 1¼ miles SE of N entrance to Menjou's Gap—125° 51½′ E, 18° 24¾′ S—Sadler Formation, 220–232′ above base.

K Dud 274—As for K Dud 271, but 302–347′ above base of Sadler Formation.

K Dul 478—Geikie Range, 3 miles N of Fossil Downs Homestead—125° 47′ E, 18° 06′ S—Fossil Downs Formation, 1,495′–1,514′ above base.

K Dup A 95—Central Bugle Gap, 3½ miles at 143° from Paddy's Spring—126° 02¼′ E, 18° 41 S—Gogo Formation; exact stratigraphic position unknown, but 5–12′ above base of small hill.

K Dup A 96—As for K Dup A 95, but 12′ above base of the hill.

K Dup 99—North central Bugle Gap area—approximately 126° 04′ E, 18° 39½′ S—probably low in Gogo Formation, but exact stratigraphic position unknown.

K Dup 120—4 miles SW of Old Bohemia Homestead—126° 07′ E, 18° 41′ S—float material, probably from the Virgin Hills Formation.

K Dup 124—Approximately 4 miles SW of Old Bohemia Homestead—126° 06′ E, 18° 42′ S—approximately 125′ above the lowest beds of the Gogo Formation exposed in the locality.

K Dup 126—As for K Dup 124, but 187–213′ above the base of the Gogo Formation.
K Dup 152—As for K Dud 149.
K Dup 155—As for K Dud 149.
K Dup 307—Pillara Range, SE of N entrance to Menjou's Gap—125° 51′ E, 18° 24′ S—near the top of the Gogo Formation.

(2) *Commonwealth of Australia Bureau of Mineral Resources Collection*

NH 9B—½ mile N of main scarp of Pillara Range, and 1 mile E of N entrance to Menjou's Gap—125° 51½′ E, 18° 24¾′ S—Sadler Formation, probably from the lower 500′.
NH 41—Limestone Billy Hills, 3½ miles S of Trig. Station L1—125° 44′ E, 18° 23½′ S—Sadler Formation, exact stratigraphic position unknown.
R 303—NW entrance to Bugle Gap, 2½ miles at 70° from Paddy's Spring—126° 03′ E, 18° 37¾′ S—Virgin Hills Formation, exact stratigraphic position unknown.
R 304—300 yards E of R 303.
R 312—Bugle Gap, at NW entrance of Wagon Pass to Old Bohemia Homestead, 4¼ miles E of Paddy's Spring—126° 05½′ E, 18° 38½′ S—Virgin Hills Formation, exact stratigraphic position unknown.
R 315—As for R 312.
RS 142—Vicinity of RS 190 (see below).
RS 147—Vicinity of RS 190 (see below).
RS 178—Vicinity of RS 190 (see below).
RS 181—Vicinity of RS 190 (see below).
RS 190—SE end of Bugle Gap, 3¼ miles at 61° from Pinnacle Spring—126° 05′ E, 18° 44½ S—Virgin Hills Formation, flanking and overlying a bioherm of the Pillara Formation. RS 190 A–D are in approximate stratigraphic order, RS 190 A being the lowest ammonoid-bearing horizon of the formation.
RS 194—Vicinity of RS 190.
RS 205—As for K Dup A 95.

(3) *University of Western Australia Collection*

B 78—E side of N entrance to Bugle Gap, approximately 4 miles E of Paddy's Spring, from "fifth hill" (hills are those to the W of the reef limestone scarp, and are numbered from N to S)—126° 05½′ E, 18° 38½′ S—Virgin Hills Formation, exact stratigraphic position unknown. Locality 66 of Teichert (1949, p. 54).
C 6–7—NE entrance to Bugle Gap, 6½ miles from Mt. Pierre Well on road to Old Bohemia road gap—approximately 126° 06′ E, 18° 37½′ S—Virgin Hills Formation, exact stratigraphic position unknown. Locality 61 of Teichert (1949, p. 54).
C 10—As for B 78, but "first hill." Locality 64 of Teichert (1949, p. 54).
C 12–14—As for B 78—top beds of "fifth hill."
C 17–26—As for B 78, but "second hill"—5′ above the sandstone bed. Locality 65 of Teichert (1949, p. 54).
C 27–32—As for 17–26, but 7′ above the sandstone bed.
C 42—On road from Salty Bore through No. 10 Bore to Long's Well, 5 miles from Long's Well approximately 125° 57′ E, 18° 34′ S—Gogo Formation, exact stratigraphic position unknown. Locality 49 of Teichert (1949, p. 54).
C 56—Strata surrounding small isolated stromatoporoid bioherm, immediately E of Gap Creek Gap, and about 2 miles N of the main reef limestones—approximately 125° 55½′ E, 18° 35′ S—Gogo Formation, exact stratigraphic position unknown. Locality 56 of Teichert (1949, p. 54).
D 5—Road from No. 10 Bore to Long's Well, 1½ miles from No. 10 Bore—125° 57′ E, 18° 37′ S—Gogo Formation, exact stratigraphic position unknown. Locality 51 of Teichert (1949, p. 54).
D 14—Fire-plough road from Salty Bore to Long's Well, 2 miles from Salty Bore—125° 56′ E, 18° 36′ S—Gogo Formation, exact stratigraphic position unknown. Locality 47 of Teichert (1949, p. 54).

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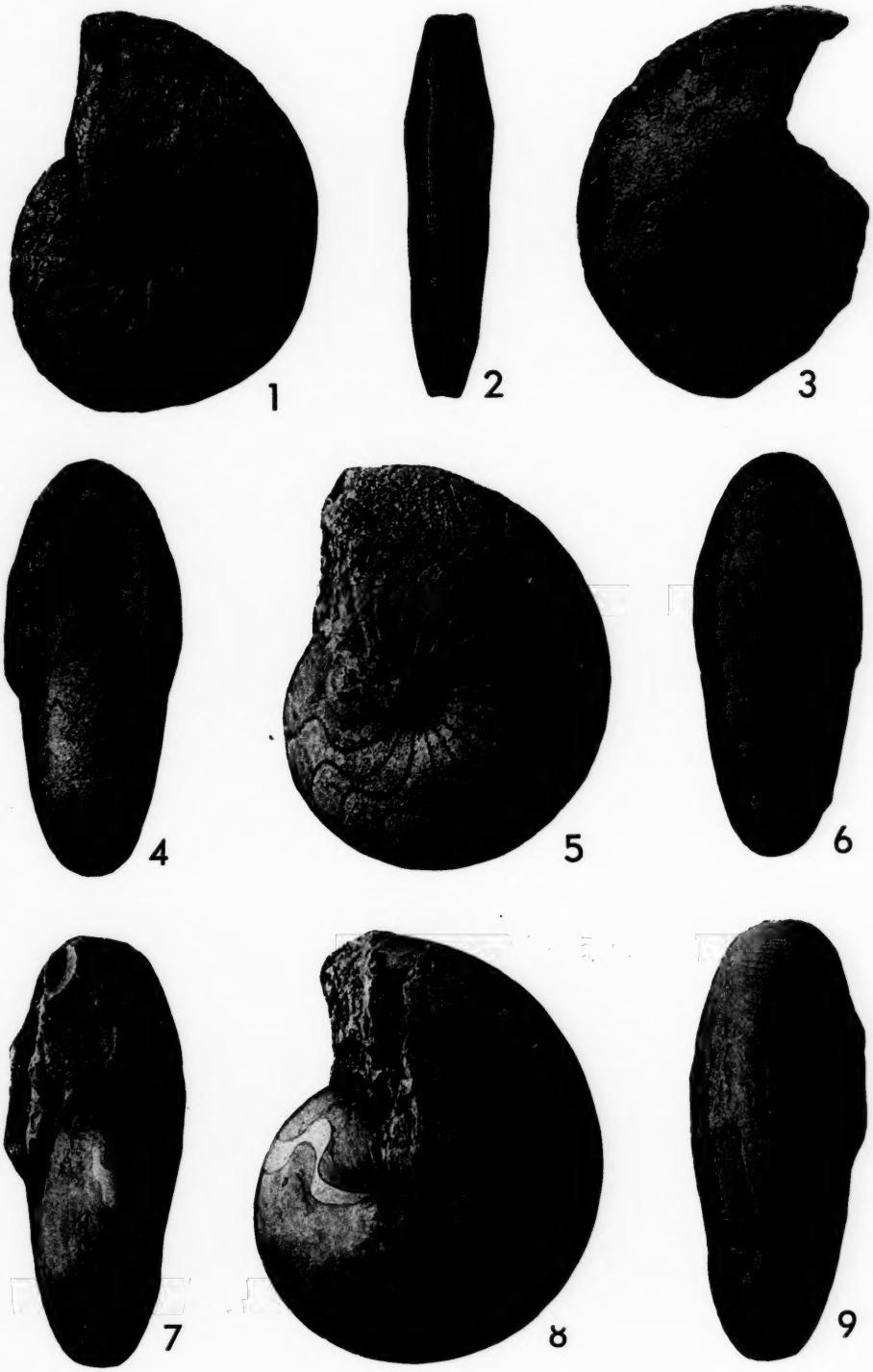
EXPLANATION OF PLATE 15

FIG. *1—Tornoceras* (*Polonoceras*) sp., figured specimen 1758, ×4½. See also Text-figs. 17A,B.

2,3—Probeloceras alveolatum Glenister, n. sp., holotype 1727, ×3. See also Text-figs. 3A,B.

4–6—Tornoceras (*Tornoceras*) *contractum* Glenister, n. sp., holotype 1753, ×2. See also Text-figs. 16B,D.

7–9—Tornoceras (*Tornoceras*) *clausum* Glenister, n. sp., holotype 1756, ×1½. See also Text-figs. 16A,C.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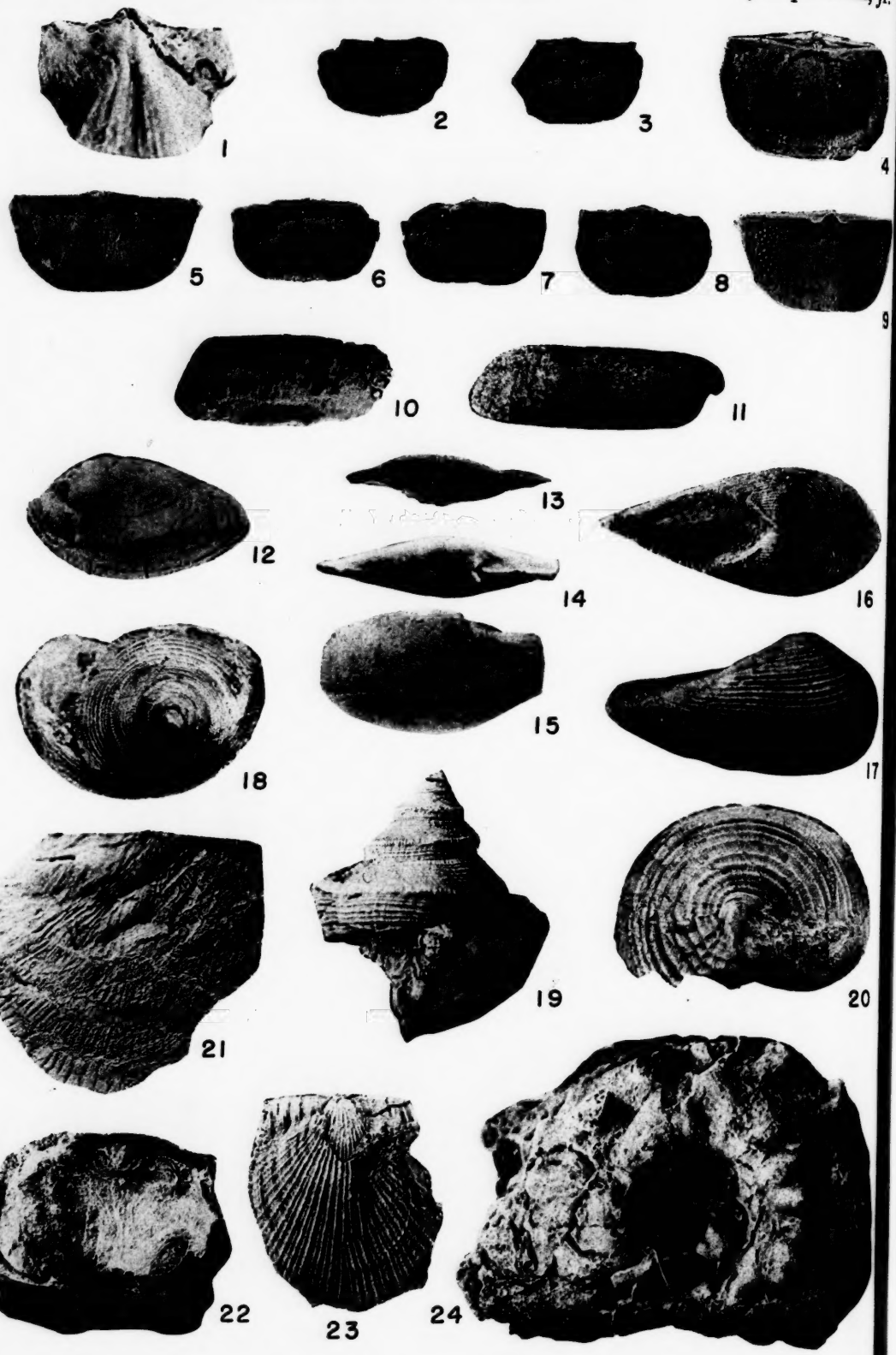
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JOURNAL OF PALEONTOLOGY, V. 32, NO. 1, P. 97–112, PL. 16, 2 TEXT-FIGS., JANUARY 1958

THE FAUNA OF THE AMES AND BRUSH CREEK SHALES OF THE CONEMAUGH FORMATION OF WESTERN MARYLAND

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ABSTRACT—A faunal list of sixty-seven species, predominantly molluscan, is presented for the two shale horizons. The Brachiopoda form the second common phylum; minor elements include rugose Anthozoa, Bryozoa, Annelida, Ostracoda, and Crinoidea. Because most specimens were obtained from drill cores and accurate depth data were available, special efforts were devoted to the recognition of biozones, but none was detected. The majority of specimens were common to both horizons; those restricted to one horizon occur infrequently within their horizon. Previous correlation by Moore et al. (1944) of the Ames and Brush Creek shales with the Stanton limestone and Bethany Falls-Swope limestones, respectively, of the Mid-continent region are substantiated.

New taxa include *Chonetes granulifer* var. *semiacanthus*, characterized by its small size and reduced number of cardinal spines, and *Chonetina verneuilianus* var. *obscurus*, small and possessing shallow sulcus. *Worthenia castlemanensis* is larger than *W. tabulata* and has less elaborate ornamentation. *Metacoceras marylandica* has a small umbilicus and isolated nodes on the umbilical shoulders. New species of Pelecypoda include: (1) *Prothyris singewaldi*, smaller, shorter, and with a more oblique posterior truncation than *P. elegans* Meek; (2) *Edmondia* (?) *pseudoreflexa*, having a distinct angle between the antero-dorsal and posterior-dorsal slopes, but otherwise resembling *E. reflexa* Meek; and (3) *Dunbarella appalachiensis*, a pectenid intermediate in characteristics between *D. knighti* Newell and *D. rectalaterarea* (Cox).

The genus *Culunana* is proposed for Pennsylvanian nuculanid taxodont pelecypods bearing an internal buttress below the umbo, a hinge plate continuous over the chondrophore, chevron-shaped anterior and rectangular posterior teeth. Possible relationships with *Polidevcia* Chernyshev are discussed. The genus *Paleyoldia* is proposed for Pennsylvanian yoldiid taxodont pelecypods possessing a posteriorly directed chondrophore, a continuous hinge plate and dorsal teeth.

EXPLANATION OF PLATE 16

FIG. *1*—*Chonetina vernueilianus* var. *obscurus*, n. var. The holotype, a pedicle valve with both extremities missing; molds of internal papillae visible on right side, ×7, USNM no. 119229.

2–9—*Chonetes granulifer* var. *semiacanthus*, n. var. *2*, nearly complete brachial valve, ×1, USNM no. 119228c. *3*, fragment of a well preserved brachial valve showing the internal detail, ×3, USNM no. 119228d. *4*, ventral view, ×2, USNM no. 119228b. *5*, large pedicle valve, ×2. *6,7*, dorsal and ventral views of same specimen, ×2, USNM no. 119228a. *8*, small pedicle valve with an unusually deep fold, ×2, USNM no. 119228e. *9*, interior view of specimen illustrated in fig. 5.

10—*Prothyris singewaldi*, n. sp. The holotype, a mold of a left valve, ×2, USNM no. 119260a.

11—*P. elegans*. Meek's original illustration for comparative purposes, ×⅔.

12,13—*Edmondia pseudoreflexa*, n. sp. Cardinal and side views of the holotype, a right valve, ×2, USNM no. 119265.

14,15—*Paleyoldia glabra* (Beede & Rogers). Cardinal and side views of the right valve of a specimen lacking the rostral extremity, ×1½, USNM no. 119271a.

16,17—*Culunana bellistriata* (Stevens). Cardinal and side view of the left valve of a well preserved specimen, ×2, USNM no. 119269a.

18–20—*Worthenia castlemanensis*, n. sp. Apical, apertural, and anapical views of the holotype, ×1, USNM no. 119244.

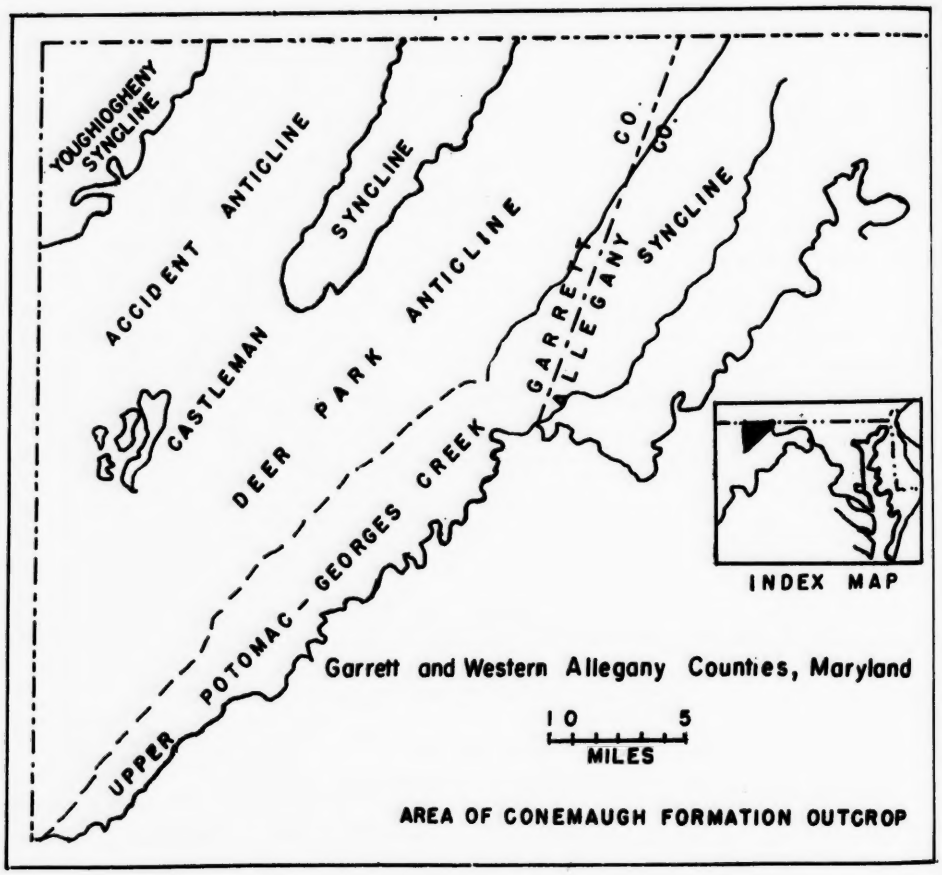
21,23—*Dunbarella appalachiensis*, n. sp. *21*, holotype, a left valve, ×2, USNM no. 119276a. *23*, paratype, an internal mold of a right valve, ×1½, USNM no. 119276b.

22,24—*Metacoceras marylandica*, n. sp. *22*, paratype, ×¾, USNM no. 119255. *24*, holotype, ×¾, USNM no. 119254.

THE fauna of the Conemaugh formation has previously been studied in Pennsylvania (Heilprin, 1886; Raymond, 1908, 1911; Theiss, 1940; Seaman, 1940, 1941, 1942; Chow, 1951), in Ohio (Meek, 1875; Mark, 1912) and in West Virginia (Price, 1914–1921; Burke, 1930). Others have investigated certain taxonomic groups in the region without attempting faunal studies. Price described the Pennsylvanian fauna of Maryland in 1913, but did not publish his results. The present paper is taken from an investigation of the two principal fossiliferous horizons in the Pennsylvanian system of Maryland.

Most of the specimens were obtained from cores of the U. S. Bureau of Mines—Maryland Department of Geology, Mines, and Water Resources cooperative core drilling programs of 1942 and 1944 in the Georges Creek and Castleman Basins. The non-paleontologic aspects of these programs have been described by Toenges et al. (1949, 1952), in which the locations of the core holes are presented. The geography of the source material is shown in Text-fig. 1. Additional specimens were collected from outcrops in the field.

Because detailed records of core footage depths were available, it was hoped that some pattern or zoning of the invertebrate species might be determined. In removing the specimens from the cores, special attention was given to depths from which they were recovered. The fossiliferous sections ranged from completely barren cores, to a maximum of twenty-two feet of fossiliferous material in one core hole, with an average of



TEXT-FIG. 1—Index map of western Maryland showing areas of outcrop of the Conemaugh Formation.

four feet of fossiliferous strata per core. Detailed plotting of the species recovered from each foot of core shows no meaningful pattern, precluding the zoning of these thin marine horizons on a faunal basis. The only permissible generalization is that intervals bearing the greatest number of species carry the greatest number of individuals as well. Those intervals bearing relatively few species usually do not have many individuals present, although in a few instances a very large number of individuals of one species occur in a single foot of core; invariably, it is a species with wide vertical distribution.

The Ames and Brush Creek shales are the two most persistent marine horizons in the Conemaugh formation of Maryland, although other, lenticular fossiliferous beds occur. The Ames shale has been correlated with the Stanton limestone of the Lansing group of the Missourian Age and the Brush Creek shale has been considered the equivalent of the Bethany Falls-Swope limestones of the lower Kansas Citian Group (Bronson Group in Missouri) of the Missourian Age by Moore et al. (1944, p. 707). The evidence of the Maryland fauna supports these correlations.

CHARACTERISTICS OF THE FAUNA

The list of species in the present collection is given in Table 1. The symbol "r" indicates less than 10 specimens present, "c" indicates 10 to 50 specimens, and "cc" indicates more than 50 specimens in the collection.

Seventy-two per cent of the fauna is common to both the Ames and Brush Creek shales. The majority of the specimens found in but one horizon are represented by too few specimens to permit a definite statement that the species is restricted to that horizon. In no instance is a species abundant in one horizon and absent in the other.

Table 1 also shows that the Ames and Brush Creek shales have a relatively high percentage of Mollusca. This high percentage has been noted by other investigators of Appalachian Carboniferous faunas, but it is in marked contrast with the faunas of the Pennsylvanian formations of the Mid-continent region, which, with the exception of the Drum limestone of Kansas, tend to have brachiopods as the largest population element. This contrast is partially explained by ecological factors. Table 2 is a comparison of the faunal composition of the Ames and Brush Creek shales as found in western Maryland and that of adjacent areas in the same horizons as reported by other investigators.

Comparisons of the faunas of the Georges Creek-Upper Potomac and Castleman Basins indicate that the same species are represented on both sides of the intervening Deer Creek anticline. Although about one-fourth of the faunas are restricted to one basin or the other, the majority of the restricted species are represented by so few specimens that little importance can be attached to their absence in the other basin. In no instance was a species found to be abundant in one basin and absent in the other.

No evidence can be found to support the belief that the two basins were isolated during the time of deposition. The basins are structural synclines formed in post-Dunkard times.

SYSTEMATIC PALEONTOLOGY

Phylum BRACHIOPODA
Class ARTICULATA
Order PROTREMATA
Superfamily STROPHOMENACEA
Family CHONETIDAE
Genus CHONETES Fischer de Waldheim, 1837
CHONETES GRANULIFER Owen, var. SEMIACANTHUS, n. var.
Pl. 16, figs. 2–9

Pedicle valve small, subquadrate, widest at hinge line; umbo inconspicuous and low with greatest convexity at midvalve; cardinal area linear with five or six pairs of spines on the margin; teeth short, prominent, without dental lamellae; apex of delthyrium with small pseudodeltidium. Valves ornamented with low, rounded, costellae having narrow, shallow interspaces; four or five costellae occur in one mm. near the anterior margin. A faint evanescent sulcus present on some pedicle valves. Brachial valve concave.

Pedicle interior with radiating rows of fine papillae near margin of shell becoming fewer, less regular, but stouter, centrally. Thin median septum extends approximately one quarter the length of the valve.

TABLE 1—SPECIES FROM THE AMES AND BRUSH CREEK SHALES

	Ames	Brush Creek
Coelenterata		
Stereostylus profundus (Milne-Edwards and Haime)	—	r
Bryozoa		
Rhombopora(?) cf. *R. lepidendroides* Meek	—	r
Annelida		
Serpulopsis insita (White)	c	c
Brachiopoda		
Lingula carbonaria Shumard	—	r
Orbiculoidea missouriensis(?) (Shumard)	r	r
Derbyia crassa (Meek and Hayden)	c	r
Chonetes granulifer var. *semiacanthus* Lintz, n. var.	cc	cc
Chonetina verneuilianus var. *obscurus* Lintz, n. var.	r	—
Juresania nebrascensis(?) (Owen)	r	—
J. symmetrica(?) (McChesney)	r	—
(?)*Marginifera wabashensis* (Norwood and Pratten)	cc	c
Linoproductus prattenianus (Norwood and Pratten)	r	r
Neospirifer dunbari(?) King	—	r
Composita ovata(?) Mather	r	r
Crurythyris planoconvexa (Shumard)	cc	c
Gastropoda		
Patellilabia tentoriolum(?) Knight	—	r
Pharkidonotus percarinatus (Conrad)	c	cc
Bellerophon crassus var. *wewokensis* Girty	c	c
Euphemites vittatus (McChesney)	cc	cc
Cymatospira montfortianus (Norwood and Pratten)	cc	cc
Glabrocingulum grayvillense (Norwood and Pratten)	cc	cc
G. ornatum (Sayre)	cc	cc
Worthenia castlemanensis Lintz, n.sp.	—	r
Shansiella carbonaria(?) (Norwood and Pratten)	r	—
Phymatopleura brazonensis (Shumard)	c	—
Amphiscapha catilloides (Conrad)	cc	cc
Strobeus primigenius (Conrad)	c	r
S. paludinaeformis (Hall)	r	r
Meekospira aff *M. percuta* (Meek and Worthen)	r	c
Girtyspira minuta (Stevens)	c	c
Donaldina stevensana (Meek and Worthen)	r	r
Pseudozygopleura sp. cf. *P. girtyi* Knight	r	r
Scaphopoda		
Plagioglypta annulistriata (Meek and Worthen)	c	c
Cephalopoda		
Pseudorthoceras knoxense (McChesney)	c	c
Tainoceras monolifer Miller, Dunbar, and Condra	r	—
Metacoceras marylandica Lintz, n.sp.	r	—
Pelecypoda		
Solemya radiata (Meek and Worthen)	r	—
S. trapezoides Meek	r	r
Solenopsis solenoides (Geinitz)	c	c
Prothyris singewaldi Lintz, n. sp.	c	c
Edmondia subtruncata Meek	r	r
E. subtruncata var. *levis* Price	—	r
E. aspenwallensis Meek	r	—
E.(?) *pseudoreflexa* Lintz, n.sp.	c	c
Paleonucula croneisi Schenck	cc	cc
Nuculopsis girtyi Schenk	c	c
N. anadontoides (Meek)	r	r
Culunana (n. gen.) *bellistriata* (Stevens)	c	c
C. attenuata (Meek)	c	c
Paleyoldia (n. gen.) *glabra* (Beede and Rogers)	c	c
Anthraconeilo taffiana Girty	c	c
Parallelodon tenuistriata (Meek and Worthen)	r	—
Schizodus wheeleri Swallow	c	r
S. curtus (Meek and Worthen)	c	c
Dunbarella appalachiensis Lintz, n. sp.	c	r

TABLE 1—(*Continued*)

	Ames	Brush Creek
Aviculopecten spp.	c	c
(?)*Acanthopecten carboniferus* (Stevens)	r	—
(?)*A. armigerus* (Conrad)	—	r
Euchondria levicula (?) Newell	r	r
Pleurophorus occidentalis Meek and Hayden	r	—
P. oblongus Meek	c	c
Astartella concentrica (Conrad)	cc	cc
A. vera Hall	c	c
Ostracoda		
Healdia sp.	c	c
Sansabella sp.	c	c
Cavellina spp.	c	c
Corvellites sp.	c	c
Bairdia sp.	r	r
Crinoidea		
Columnals	cc	cc

TABLE 2—COMPARISON OF FAUNAS

Author	Date	Total Species	Horizon	Locality	Brachiopoda	Gastropoda	Pelecypoda
Raymond	1911	49	Brush Creek	Penna.	13	15	8
Raymond	1911	48	Ames	Penna.	17	11	7
Price	1914	52	Brush Creek	W. Va.	11	9	22
Price	1914	48	Ames	W. Va.	7	16	22
Burke	1930	40[a]	Ames	W. Va.	20	4	—
Theiss	1940	76	Ames	Penna.	31	25	11
Seaman	1940	76[b]	Ames	Penna.	28	14	14
Seaman	1942	119[b]	Brush Creek	Penna.	19	29	31
Chow	1951	50	Mill Creek	E. Penna.	10	4[c]	32
Lintz	1958	57	Brush Creek	Maryland	9	15	22
Lintz	1958	60	Ames	Maryland	10	15	25

[a] 7 Species of Crinoidea.
[b] Pisces omitted.
[c] Abundant unidentified microgastropoda.

Brachial interior with concentric rows of papillae. A small cardinal process with four radiating ridges on dorsal side nearly fills the delthyrium; cardinal process buttressed by laterally directed ridges which reinforce the dental sockets. A very small shallow depression anterior to the cardinal process. Median septum sharp and thin, extending from anterior margin of the depression to the center of the valve. Two low, broad, slightly divergent mounds on both sides of the septum, apparently serving as points of attachment for muscles.

Discussion.—This is the most common brachiopod occurring in the Pennsylvanian of western Maryland, being abundant in the Ames and Brush Creek shales. It was found in nearly all wells of both basins and had the greatest vertical distribution within the cores of any brachiopod. Several hundred specimens were obtained.

Dimensions (in mm.) of the several illustrated specimens:

USNM no.	Width	Length	Depth	Cardinal Spines	Cardinal-lateral angle
119228a	11.5	6.6	—	—	89°
119228b	11.7	7.8	2.0	5 pr.	90° (est.)
119228e	8.6	5.5	1.4	6 pr.	98°
—	10.0	5.3	—	—	78° (Figs. 5,9)

The angle formed by the lateral and cardinal margins varies. Several specimens, such as that illustrated in plate 16, figures 5,9 have somewhat produced extremities forming an acute angle, but the majority of the individuals have this angle near 90°. Figure 8 shows a specimen whose hinge line is shorter than the greatest width.

This variety is smaller than *C. granulifer* Owen and has only five or six pairs of cardinal spines whereas Owen's species has 10 to 12 pairs of spines on the cardinal margin (Dunbar & Condra, 1932, p. 139). Specimens of *C. granulifer* in the University of Nevada collections from Kansas and Oklahoma have hinge line lengths of 23 to 33 mm. and bear 7–10 pair of spines. Another group from the Cherokee shale at Plattsburgh, Kansas, are smaller with the hinge lines averaging about 14 mm. long, and have the lateral and cardinal margins intersecting at approximately 90° producing a quadrate shell. The latter group bears five to six pairs of cardinal spines and resembles that specimen illustrated by Dunbar & Condra (1932) on their plate 18, figure 6. The Maryland specimens in addition to their small size are distinguishable by the reduced number of cardinal spines and non-attenuated cardinal extremities. While there is an occasional specimen with this tendency in the Maryland collection (pl. 16, figs. 5,9) the great majority are subquadrate.

Dunbar & Condra (1932, p. 146) state that most if not all the *Chonetes* species have minute tubular spines on both valves, and that the bases of these spines should be visible in well preserved material. These small spine bases cannot be discerned on the material in the University of Nevada collections, nor in the Maryland specimens.

Of the described varieties of *C. granulifer*, the Maryland specimens most nearly resemble *C. granulifer armatus* Girty (1911, p. 127). Differences between the two varieties appear to be of degree rather than kind. Dunbar & Condra (1932, pl. 21, figs. 1–4) show individuals with distinct but shallow sulci. However, in their description of the Nebraska material they state (p. 146) that the sulcus is not present in all valves. In the Maryland specimens the sulcus is present in a few specimens, but is lacking on most. When present, it is faint, shallow, and not conspicuous. The dimensions of Nebraska specimens of *C. granulifer armatus* are given by Dunbar & Condra (1932, p. 146) as "15 mm. in breadth and 11 mm. in length, though an average specimen is only 13 mm. wide and 9 mm. long." *C. granulifer semiacanthus* is thus approximately the same size as *C. granulifer armatus*. Another point of likeness between these two varieties is the ornamentation. In both instances the radial costellae are poorly defined with the unaided eye, but readily seen with magnification. The range of *C. granulifer armatus* is reported by Dunbar & Condra (1932, p. 147) to be restricted to the Desmoinesian and the lower half of the Kansas City group of the Missourian stage. The range of *C. granulifer semiacanthus* is not known, but there is no distinction between the groups of shells from the Ames and Brush Creek shales. Holotype: USNM no. 119228a; paratypes nos. 119228b–e. Type locality: USBM core hole 14, Georges Creek Basin, Allegany County, Maryland.

Genus CHONETINA Krotow 1888

CHONETINA VERNEUILIANUS (Norwood & Pratten) var. *obscurus*, n. var.

Pl. 16, fig. 1

Small chonetids with heavy conspicuous pedicle umbo bearing a well defined, narrow sulcus extending to the anterior margin. Sulcus bordered by folds diverging at about 30°. Four pairs of spines on the cardinal margin. Length slightly more than three-fifths the width. Ornamentation lacking on umbo and concave umbonal slopes, but 35–40 broad, flat costellae are visible on the lateral and anterior margins. Interspaces shallow and one-fourth to one-fifth the width of the costellae. Pedicle valve with interior radial papillae.

Discussion.—Two small specimens in the present collection do not quite agree with the descriptions given by Dunbar & Condra (1932, p. 158) for *C. verneuilianus* (Norwood & Pratten). The differences are of degree rather than kind. For that reason and because of the few specimens a new variety rather than new species is proposed.

Like *C. verneuilianus*, this variety has moderate convexity, the umbo is pronounced, and there are but four cardinal spines. Unfortunately the preservation is

too poor to determine the direction of the spines.

C. verneuilianus obscurus differs from the typical form in its small size, in having a relatively shallow sulcus, and in details of ornamentation. Dunbar & Condra (1932, pl. 19, figs. 14–17) illustrate individuals of *C. verneuilianus* having a narrow deep sulcus with slightly divergent folds on both sides. The Maryland specimens have a sulcus which is definite and distinct, which is narrow and between two slightly divergent folds, but which lacks the depth of the sulcus typical of *C. verneuilianus*.

Norwood & Pratten (1854, p. 26) give the dimensions of the type specimens of *C. verneuilianus* as "length 7 mm., breadth 12 mm." Dunbar & Condra (1932, p. 159) find specimens from the Mid-continent range up to 14 and 15 mm. in width. The new variety is characterized by its small dimensions (given in mm.):

Specimen	Width	Length	Ratio W/L	Remarks
1	4.2	2.7	0.64	Illustrated
2	1.4	1.0	0.71	Internal mold

The costellae on the present specimens are poorly defined, having very shallow and narrow interspaces. The umbonal areas are without ornamentation, but on the anterior and lateral slopes 35–50 costellae are present. Norwood & Pratten's species (1854, p. 26) is "covered with about 100 ribs, very fine and dichotomous."

Plate 16, figure 1 shows a subquadrate individual. It is possible this individual was slightly alate and the cardinal extremities lost by abrasion. The internal mold does not clearly demonstrate produced cardinal extremities. The suggestion that the hinge line was longer is given by the rows of internal papillae which are truncated by the core bit. It does not appear likely, however, that the lateral margins were concave.

The present specimens were recovered from core holes GC 5 and CB 34, in each case from the Ames shale. Raymond (1911, p. 95) lists *C. verneuilianus* from the Vanport, Brush Creek and Pine Creek shales. Seeman (1940, 1942) does not list *C. verneuilianus* in his reports.

Holotype: USNM no. 118229. Type locality: USBM core hole 5, Georges Creek Basin, Allegany County, Maryland.

Phylum MOLLUSCA
Class GASTROPODA
Genus WORTHENIA Koninck, 1883
WORTHENIA CASTLEMANENSIS, n. sp.
Pl. 16, figs. 18–20

Moderately large conispiral gastropods of seven to eight whorls with a turreted spire. Whorl profile with two angulations, the upper one acute, bearing the selenizone; the lower one obtuse, seen only on last whorl. Outer lip with broad V-shaped sinus. Selenizone narrow, carinate, and sharply nodose. Parietal lip arcuate and with thin inductura. Aperture trapezoid. Ornamentation of sharp revolving lirae with very fine incremental growth lines at maturity, and with slightly reticulated appearance on second and third whorls only. Shell structure of two layers, inner thicker than outer. Pleural angle 76°.

Discussion.—This species is based on a single well preserved but slightly crushed specimen. The complete outer lip with slit is missing. The specimen is 41 mm. from spire to anterior tip. Measurement of the width has no significance due to the crushing, but is estimated to have been approximately 33–35 mm.

Worthenia castlemanensis is distinguished from the more widely known *W. tabulata* (Conrad) by its larger size and less ornate ornamentation. The revolving lirae are sharply defined, continuous, and with a slight nodose appearance. They are much more prominent than the very fine growth lines. The selenizone lacks revolving ornamentation and bears only small nodes, 12 occurring in 10 mm. near the end of the outer whorl. The anapical ornamentation lacks any suggestion of reticulation. According to Dr. Knight, this is the most distinguishing characteristic of the new species, for he reported he had never seen this previously in American Worthenias (J. B. Knight, oral communication, July 1951).

The holotype is from the Brush Creek formation in U. S. Bureau of Mines core hole CB 9, 2½ miles S. 13° E. of the intersection of state route 495 and U. S. Route 40, Grantsville, Maryland. It is named for the Castleman Basin.

The holotype is designated as USNM no. 199244. Type locality: USBM core hole 9, Castleman Basin, Garrett County, Maryland.

Class CEPHALOPODA
Subclass NAUTILOIDEA
Genus METACOCERAS Hyatt, 1883
METACOCERAS MARYLANDICA, n. sp.
Pl. 16, figs. 22,24

Tarphyceraconic nautiloid cephalopods with nodes on the venterolateral and umbilical shoulders. Whorls enlarging rapidly so that three quarters of the size is due to the outer volution. Umbilicus open, of medium size. Whorl profile subquadrangular, height about two-thirds the width. Greatest width at umbilical shoulders. Dorsum with central impressed zone about one third of total width and with gently dipping lateral umbilical walls. Umbilical shoulder almost a right angle, rounded; lateral wall straight, sloping in gently towards the center. Venter slightly arched, but with flat central area. Nodes on ventral margins paired, 12–13 mm. apart, directed laterally and slightly adaperturely. Nodes on umbilical shoulders paired, less strongly developed and spaced about 8 mm. apart. No ribbing or nodular elongation between ventrolateral margin and umbilical shoulder. Shell material thick, nodes greatly reduced on internal molds.

Discussion.—This species is based on fragments of three individuals. The holotype, split longitudinally near the venter, exhibits slightly more than one whorl. The paratypes are whorl fragments, possibly of the living chamber. An internal mold of a half whorl split longitudinally possibly belongs to this species. No sutures, siphuncles, or apertures are preserved.

The holotype has a greatest diameter of 79.6 mm. The illustrated paratype is 44 mm. wide and 27.3 mm. high.

M. marylandica differs from *M. sangomonense* (Meek & Worthen, 1866, p. 368, pl. 29, fig. 3–3b) in the relatively small umbilicus and in having nodes on the umbilical shoulders. *M. perelegana* Girty (Girty, 1915, p. 244, pl. 30, figs. 5,6) is the only other species of *Metacoceras* having nodes on the umbilical shoulders, but these nodes are connected with those of the ventrolateral angulations by low ribs in at least part of the outer volution.

The specimens were collected from outcrops of the Ames shale at mine no. 19 (U. S. Bur. Mines Tech. Paper 725) just east of Mt. Savage, Allegany County, Maryland.

The holotype is USNM no. 119254, the illustrated paratype is USNM no. 119255. Type locality: Mine 19, USBM Technical Paper 725, Georges Creek Basin, Allegany County, Maryland.

Class PELECYPODA
Order PRIONODESMACEA
Section PALAEOCHONCHA
Family SOLENOPSIDAE
Genus PROTHYRIS Meek, 1869
PROTHYRIS SINGEWALDI, n. sp.
Pl. 16, fig. 10

Small transverse, compressed pelecypods with length slightly more than twice the height. Dorsal and ventral margins straight, subparallel; posterior margin straight, obliquely truncated, sloping about 55°. Anterior margin rounded to the anterior notch, which is approximately at midheight, then sharply rounded about the anterior lobe, which is gently convex to the umbo. Umbos near anterior end, depressed, inconspicuous. Shell with a narrow posterior and greater anterior gape. Cardinal margin with shallow depression and gentle ridge on anterior lobe. Ornamentation of fine striae parallel to the ventral margin and over anterior lobe. Striae turning abruptly upward and widening to form rounded shallow depressions parallel to the posterior margin with broad rounded low elevations of equal width in the interspaces.

Discussion.—Meek proposed the genus *Prothyris* in 1869 (Meek, 1869, p. 172) without referring to it any named species. In 1871, he described *P. elegans*, which he designated the type species (Meek, 1871, p. 8, pl. 1, fig. 3). He included *P. meeki* (Winchell) in his genus in his discussion of 1871, although Winchell did not publish his description until 1875.

There are sixteen specimens in the Maryland collections which were first thought to be conspecific with *P. elegans* because their ornamentation is identical. However, closer inspection shows (1) they are about one-half the size of Meek's species; (2) *P. elegans* has a length/height ratio of 3.2, while the ratio for the Maryland shells is 2.3; and (3) the

obliquely truncated posterior is more nearly vertical in *P. elegans. P. meeki*, on the other hand, is noticeably more convex, with a shallower anterior notch, and with more prominent umbos.

Dimensions in mm. of selected specimens:

Specimen	Length	Height	L/H Ratio	Obliquity of truncated posterior
1 (Holotype)	13.8	6.0	2.3	62°
2	10.8	4.4	2.45	60°
3	15.0 (est.)	7.0	2.12	61°

The shell in this genus, being very thin, is easily distorted in burial, and is usually poorly preserved. Some of the specimens are internal molds. In none are both valves together.

The name is given in honor of Dr. J. T. Singewald, Jr., Director, Maryland Department of Geology, Mines, and Water Resources.

The specimens occur in both the Ames and Brush Creek shales and in the Georges Creek Basin where they were recovered from core holes GC 5 and GC 15. In the Castleman Basin they were found in core holes CB 3, CB 12, CB 17 and CB 34.

The holotype is designated as USNM no. 119260. The paratypes are USNM 119260a, b. Type locality: USBM core hole 3, Castleman Basin, Garrett County, Maryland.

Family GRAMMYSIIDAE
Genus EDMONDIA Koninck, 1844
EDMONDIA(?) PSEUDOREFLEXA, n. sp.
Pl. 16, figs. 12,13

Small, equivalved, transversely elongated pelecypods having acutely rounded anterior and posterior ends. Anterodorsal margin sloping from the umbonal region then sharply round at the anterior margin; ventral margin regularly elliptical; posterior end acutely rounded; posterodorsal margin long, even, nearly straight. Angle between posterodorsal and anterodorsal slopes 135°. Valves compressed. Umbos low, inconspicuous, situated about one-third of shell length from the anterior end. Ornamentation of concentric growth lines. Shell thin. Interior of valve unknown.

Discussion.—This small species was referred to *E. reflexa* Meek 1872 (p. 213, pl. 10, fig. 6a,b; pl. 4, fig. 7) in preliminary identifications. However, upon rechecking it was found to differ from that species in the shape of the dorsal margin. *E. reflexa* has a nearly straight dorsal margin and the anterior and posterior margins are evenly rounded; the ventral, eliptical. In contrast, the present species has a distinct angle between the anterodorsal and the posterodorsal slope. In *E. reflexa* the umbos rise above the hingeline while in the new species, they are barely elevated above the hingeline. Size of the individuals and the ornamentation of both species is similar.

Due to the lack of knowledge of the internal characters this new species is only questionably referred to *Edmondia* De-Koninck. However, the class similarity to *E. reflexa* warrants the provisional assignment.

Dimensions (in mm.) of several individuals follow:

Specimen	Height	Length	Width	Ratio H/L	Ratio L/W	Ratio H/W
1 (Holotype)	7.6	14.0	3.2*	1.84	8.74	4.75
2	7.0	11.3	—	1.59	—	—
3	7.1	14.8	1.7	2.08	8.70	4.17
4	9.2	16.8	2.0	1.83	8.39	4.60
5	6.2	14.8	—	2.38	—	—

* Both valves.

E. pseudoreflexa is represented by twenty-two specimens in the Maryland collections; about half are from the Ames, the other half from the Brush Creek shale. They were obtained from core holes GC 2, GC 5, GC 10, GC 14, GC 15, GC 20, CB 1, CB 3, CB 5, CB 6, CB 12, CB 18.

USNM no. 119265 is designated as the holotype. Type locality: USBM core hole 5, Castleman Basin, Garrett County, Maryland.

Section TAXODONTA
Family NUCULANIDAE
Subfamily NUCULANINAE
Genus CULUNANA, n. gen.

Paleozoic nuculanids bearing a subvertical internal buttress below the umbo and with hinge plate continuous over the top of the chondrophere. Anterior teeth chevron-shaped, posterior teeth rectangular. Ventral interior margin smooth. Shell thick. Type species: *Leda bellistriata*, Stevens, 1858.

Discussion.—Nuculana Link (1807) (= *Leda* Schumacher 1817) has been used as the genus to which various upper Paleozoic thick shelled taxodont pelecypods with produced posterior ends have been referred. Studies of the dentition of these forms by Hall (1858, p. 717, pl. 29, figs. 6a–d) and Girty (1915, p. 120 ff.) show some similarities with the dentition of modern *Nuculana*. However, the latter has chevron-shaped teeth, while the posterior teeth of the upper Paleozoic species are rectangular. The Paleozoic specimens differ from *Nuculana* also in the possession of a conspicuous internal buttress under the umbo. This feature was illustrated as early as 1858 by James Hall, but there is no discussion of it in the literature until Girty mentioned it in 1915. Girty noted that the "oblique internal ridge," as he called it, appeared to be characteristic of all Paleozoic species of the genus.

The genotype of *Nuculana, Arca pernula* Muller 1779, is a recent species from the North Atlantic. Examination of specimens identified as *N. pernula* in the collections at Stanford University discloses no evidence of even a faint internal ridge or buttress. The chondrophore is very broad and shallow, dividing the hinge plate into anterior and posterior segments. The teeth are chevron-shaped with the exception of five posterior teeth under the umbo which are rectangular. These teeth are dorsal to the chondrophore and there is a suggestion that the lower arms of the chevrons have been squeezed out by that structure.

The Pennsylvanian specimens, upon which the new genus is based, possess a chondrophore of subequilateral trigonal shape. The ventral margin is gently rounded and protrudes very slightly into the body cavity. The chondrophore does not extend entirely through the hinge plate, which is continuous dorsal to it.

The anterior and posterior elements of the hinge plate of *N. pernula* are quite uniform in width. This is in contrast with *Culunana* which has a double tapering anterior element. The posterior portion increases slightly and uniformly in width towards its posterior end.

Except for the five posterior teeth under the umbo, *N. pernula* has chevron-shaped teeth. *Culunana* has chevron-shaped anterior teeth, but the posterior teeth are rather blocky and rectangular for the most part, although some chevron-shaped teeth occur near but not at the posterior end of the posterior hinge plate. The posteriormost teeth are subconical or amorphous. The anterior teeth are relatively large in the middle of the series, with tooth size of individual teeth diminishing as the extremities are approached. Tooth size of the posterior teeth tends to follow the same pattern, but the width of the tooth does not increase markedly; the increase in size results, therefore, from greater massiveness, probably as a function of increase in length of the teeth.

The buttress originates under the umbo and extends towards the ventral margin, usually with slightly posterior obliquity. Very pronounced in the specimens from the Mid-continent region, it is less well developed in the specimens in the present collection from western Maryland. It is present to my knowledge in *C. bellistriata* (Stevens), *C. arata* (Hall), *C. prolongata* (Morningstar), and *C. meekana* (Mark). *N. obesa* (White), insofar as I can determine from illustrations, lacks a buttress.

Chernyshev (1951, p. 25) proposed the genus *Polidevcia* for certain nucluanids from the Carboniferous of the Donetz Basin. His description of *Polidevcia* differs principally

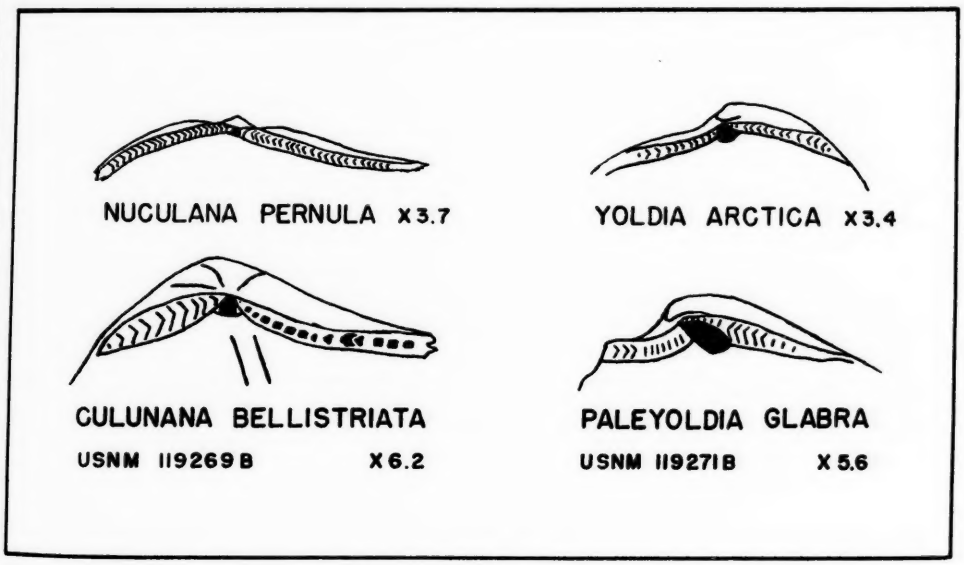
from the foregoing description of *Culunana* with the short statement "Chondrophore absent." Chernyshev used *P. karagandensis* Chernyshev as the type species. The interior characteristics of this species are undescribed. Externally *P. karagandensis* is similar to *C. bellistriata* (Stevens) and *Nuculana attenuata* Fleming, which are known to possess chondrophores. Drs. Newell (oral communication, Dec. 23, 1955) and Elias (personal communication, Nov. 28, 1955) anticipate the presence of the chondrophore in *P. karagandensis* when the interior structures are known. Once this is determined to be true, under the rules of nomenclature, *Culunana* would then be set aside as a junior synonym.

The name *Culunana* is an anagram of *Nuculana*.

CULUNANA BELLISTRIATA (Stevens) 1858
Pl. 16, figs. 16,17; Text-fig. 2

Leda bellistriata Stevens, 1858, Am. Jour. Sci., 2nd Ser., v. 25, p. 261.
Leda bellastriata Hall, 1858, Geol. Survey Iowa, v. 1, pt. 2, p. 717, pl. 29, figs. 6a–c.
Nuculana bellistriata White, 1884, Ind. Dept. Geol. and Nat. Hist., Thirteenth Ann. Rept., pt. 2, p. 146, pl. 31, figs. 8,9.
Nuculana bellistriata Beede, 1900, Kans. Univ. Geol. Survey, v. 6, p. 148, pl. 20, figs. 14–14b.
Leda bellistriata Girty, 1915, U. S. Geol. Survey, Bull. 544, p. 122, pl. 14, figs. 1–9a.
(*non*) *Leda bellistriata* Sayre, 1930, Kans. Geol. Survey, Bull. 17, p. 106, pl. 18, figs. 7–7c.
Leda bellistriata Morse, 1931, Ky. Geol. Survey, v. 36, p. 315, pl. 50, figs. 8–15.
Leda bellistriata Chow, 1951, Pa. Topog. and Geol. Survey, Bull. G 26, p. 25, pl. 3, fig. 3.

Medium-sized transverse pelecypods with taxodont dentition. Anterior margin evenly rounded, ventral evenly but more gently rounded, posterior subtruncate, sharply rounded. Dorsal margin straight, slightly carinate posteriorly. Umbos anterior to midlength of the valve, conspicuous, inflated, approximate, and very slightly opisthogyrate. Lunule small, lanceolate; escutcheon large, sharply defined by a narrow raised ridge. Ornamentation of irregularly spaced sharp concentric lirae, averaging three per mm. on the median portion of the valve, but becoming ill-defined and absent at the anterior and posterior margins. Posterior tooth row with nine rectangular teeth anteriorly that decrease in size toward the umbone, but continue dorsal to the chondrophore. Behind these are three to four chevron-shaped teeth and two to three subconical to amorphous teeth at the end of the row. Anterior tooth row with ten chevron-shaped teeth that are largest in the



TEXT-FIG. 2—Comparison of modern and Pennsylvanian nuculanid dentitions.

middle of the series and decrease in size toward both ends of the row. Hinge plate continuous over the subequilaterally trigonal chondrophore which projects slightly into the body cavity. The sides of the chondrophore diverge at an angle of about 73°. A subumbonal, internal buttress, present on some specimens, extends toward the ventral margin with a slight posterior obliquity. Ventral margin smooth; shell very thick.

Discussion.—The Maryland specimens are referred to *Leda bellistriata* Stevens on the basis of their external features and the proximity to Stevens' type locality in Columbiana County, Ohio, 150–175 miles to the west. Stevens did not illustrate his specimens, and, in addition to the Ohio locality, mentioned a second locality at Danville, Illinois. The first illustrations of this species were given by Hall (1858, pl. 29, figs. 6a–c) and show a pronounced interior buttress. Hall's specimens were from Illinois. Other specimens identified as *Nuculana bellistriata* (Stevens) from Oklahoma, Kansas, and Texas have pronounced buttresses. Girty (1915, p. 124) noted this feature in all species of paleozoic nucluanas. It came as a surprise to find the buttress poorly developed in the Maryland specimens. Of the four specimens showing internal characteristics, the buttress is low and rounded, but unmistakably present on one specimen; it is faint and short on a second specimen; and is lacking on the other two specimens. Dr. Maxim K. Elias (personal communication, Dec. 1954) has suggested that the buttress is a gerontic feature and not a valid basis for classification. This suggestion does not accord with the evidence afforded by the specimens before me. The specimens without the buttress are intermediate in size, while the smallest of the four has the best developed buttress and the largest a faint buttress. Since the structure is so well developed in the Mid-continent specimens, its poor development or absence in the Maryland specimens suggests a geographic variation or possible subspecies. The variation between the faint and missing buttresses is suggestive of the gradational nature of geographic variation.

The external features have been described from approximately 25 specimens of which only one, from the Ames shale, is complete and undeformed. It is surprising that so many specimens are crushed when the relative thickness of the shell is considered. Other apparently well preserved individuals have been truncated by the core bit. Dimensions (in mm.) of the undeformed specimen compared with those of other authors are:

Specimen	Height	Length	Width	Ratio H/L	Ratio L/W	Ratio H/W
Ames sh.	10.2	21.3	8.2	2.10	2.59	1.24
Wewoka sh.						
Girty 1915	10.3	18.5	7.8	1.79	2.45	1.37
Beede 1900	14.0	27.0	10.0	1.93	2.70	1.40
Morse 1931	12.2	23.2	—	1.90	—	—

The length of the rostrum appears to vary in this species resulting in a variation of the H/L ratio. *C. arata* (Hall) has depressed umbos and coarser ornamentation. *C. jillsoni* (Morse) is about one half the size of *C. bellistriata* and has a greatly reduced rostrum and coarser ornamentation. *C. prolongata* (Morningstar) from the Pottsville formation is similar to *C. bellistriata*, but the specimens available to me were not of sufficient calibre to warrant comparisons.

C. bellistriata is a common fossil in both the Ames and Brush Creek shales of the Conemaugh formation and occurs in the Georges Creek and Castleman Basins. It was recovered from nearly every core hole examined.

USNM no. 119269a,b.

Subfamily YOLDINAE
Genus PALEYOLDIA, n. gen.

Medium to small taxodont pelecypods with narrow, posteriorly directed chondrophore. Umbos depressed, opisthogyrate; posterior produced, rostrate. Valves com-

pressed, gaping anteriorly. External ornamentation lacking, or of sharp shallow concentric striae best developed over medial portion of the valve and becoming obscure at the anterior margin and rostrum. Chondrophore directed posteriorly, hinge plate continuous and with dorsal teeth. Interior ventral margin smooth. Type species: *Yoldia glabra* Beede & Rogers, 1898.

Discussion.—This genus is proposed to accommodate some and possibly most of the Carboniferous species previously referred to *Yoldia* Möller, 1842. Hind (1896–1900, p. 194) suggested that *Yoldia* be restricted to at least the post-Paleozoic eras, but failed to establish a genus to implement his idea. No subsequent workers have followed his suggestion.

Möller (1842, p. 91) placed *Nucula arctica* Gray and *Nucula myalis* Couth in his new genus, but did not designate a type species. He misidentified Gray's species, so that his specimens were homonyms of *Nucula arctica* Gray. The type species was finally designated as *Nucula arctica* Gray by Miss Gardner (1916, p. 518). Discussion on *Yoldia* by Stewart (1930, pp. 59–60) and Grant & Gale (1931, p. 127) omit reference to Miss Gardner's work, but agree by other lines of reasoning that *Nucula arctica* Gray is the type species for *Yoldia*. Mossevitch (1928) has described the amount of variation known in the species and shown the variation to be a function of the different environments in which it has been found.

The greatest difference between *Yoldia* and *Paleyoldia* is in the shape and character of the chondrophore. That of *Yoldia* approaches the equilateral triangle. The two dorsal sides are a little convex while the ventral side projects into the body cavity but slightly. The floor of this chondrophore slopes so that the shallowest part is at the dorsal apex while the broad ventral side is considerably depressed below the hinge line. When both valves are together, the shape of the resilium approaches a tetragonal pyramid.

The chondrophore of *Paleyoldia* resembles that of *Yoldia* only insofar as the projection of its ventral margin into the body cavity is limited. It is narrow, with the sides diverging approximately 35°. The extreme obliquity is especially noteworthy; a line through the apex and the midpoint of the ventral margin intersects a vertical line at an angle of approximately 50°. The posteroventral portion of the chondrophore is quite convex, while the dorsal portion is concave. The floor slopes from the apex, in much the same manner as that of *Yoldia;* however, the slope is gentler in *Paleyoldia.*

Yoldia arctica (Gray) has 14–15 anterior teeth and 11 posterior teeth. The three anterior teeth under the beak are subconical, as is the anteriormost tooth. The intermediate anterior teeth are chevron-shaped at the base, but are quite long and rise to a conical spire which usually occurs over the apex of the chevron. Teeth are lateral but not dorsal to the chondrophore. The posterior teeth are also chevron-shaped with the exception of the posteriormost tooth which is subconical. Like the anterior teeth the posterior teeth rise to a conical spire above the chevron apex.

In *Paleyoldia* only a few teeth are chevron-shaped. Anterior teeth dorsal to the condrophore are rectangular, some of the teeth anterior to the chondrophore are chevron-shaped, but they are not symmetrical, having a ventral segment approximately three times as long as the dorsal one. The apex of the chevron is directed towards the chondrophore. The remaining anterior teeth are reduced in size and are rectangular to subconical in shape. There are 13–14 anterior teeth.

There are 11 teeth on the posterior row. All are rectangular except the three posteriormost teeth which are chevron-shaped, with the apex directed towards the chondrophore. The arms of the chevrons are subequal. The hinge plate is sharply curved. When the hinge characteristics of *Yoldia arctica* (Gray) are compared with those of *Paleyoldia glabra* (Beede & Rogers) it is apparent that the teeth of *Paleyoldia* appear to be crowded, and that the hinge plate of the paleozoic genus is continuous over the chondrophore, whereas in *Yoldia* it is interrupted by the chondrophore.

The two specimens of *P. glabra* before me that show internal characteristics are both fragments, precluding any determination of details of the pallial line.

Unfortunately, there has been no opportunity to examine specimens of other Car-

boniferous species commonly referred to *Yoldia*, and any reassignment of those species must await a study of their internal characteristics.

PALEYOLDIA GLABRA (Beede & Rogers) 1898

Pl. 16, figs. 14,15; Text-fig. 2

Yoldia glabra Beede & Rogers, 1898, Kans. Univ. Quart., v. 8, no. 3, p. 133, pl. 34, figs. 4a,b.
Yoldia glabra Beede, 1900, Kans. Univ. Geol. Survey, v. 6, p. 153, pl. 21, figs. 4a,b.
Yoldia glabra Girty, 1915, U. S. Geol. Survey, Bull. 544, p. 126, pl. 13, figs. 9–15.
Yoldia glabra Sayre, 1930, Kans. Geol. Survey, Bull. 17, p. 107, pl. 9, figs. 1–3.

Medium-sized transverse pelecypods with taxodont dentition. Anterior margin rounded, ventral margin gently convex with slight constriction just posterior of the umbo. Posterior rostrate, constricted, rounded. Dorsal margin rising to a sharp thin keel at hinge line anterior to the umbos, continuing posterior of beak through an obscure escutcheon but decreasing in prominence. Valves very compressed. Umbos small, depressed, opisthogyrate, located slightly anterior of the midpoint. Rostrum with low sharply rounded ridge commencing posterior of umbo and continuing parallel and just below the dorsal margin to the posterior extremity forming a subcircular gape about 1 mm. in size.

Interior with obliquely directed chondrophore which intersects a vertical line through the umbos at approximately 50°. Apex of chondrophore is posterior. Chondrophore projection into body cavity very slight. Anterior teeth 12–14, six small teeth dorsal to the chondrophore. The first tooth before the chondrophore is rectangular and thin. Next three teeth chevron-shaped with ventral arm three times as long as the dorsal arm. Apex of chevron posteriorly directed. Four anteriormost teeth rectangular to conical, all reduced in size. Eleven posterior teeth; eight teeth on the curved portion of the hinge plate rectangular and slightly irregularly directed. Three posteriormost teeth chevron-shaped, with chevron arms subequal and apices directed anteriorly. Ornamentation of regularly spaced shallow, concentric striae with flat interspaces. Approximately four striae per mm. Shell thin.

Discussion.—The 16 specimens referred to this species are fragmental. The very thin shell was readily distorted. The interiors are described from two specimens, one of which has a complete hinge plate, but the other lacks most of the posterior teeth.

Beede & Rogers' description (1898, p. 133, pl. 34, figs. 4a–b) is not complete and unfortunately is accompanied by an illustration in which most of the detail is lost. Girty's (1915, p. 126, pl. 13, figs. 9–15) illustrations of this species are in agreement with the present specimens. However, Girty's identification was made with reserve. Sayre (1930, p. 107, pl. 9, figs. 1–3) illustrates an individual similar to those of Girty and to the specimens from Maryland. Two small groups of shells from Oklahoma identified as *Y. glabra* Beede and Rogers were loaned by Dr. Maxim K. Elias from the collections of the Nebraska Geological Survey. One group is from the Wewoka formation near Ada, while the other is from the Otterville limestone north of Gene Autry. They appear to be conspecific with the Maryland shells.

Dimensions (in mm.) of the various specimens follow:

Specimen	Height	Length	Width	Ratio H/L	Ratio H/W	Ratio L/W
1 (illus.)	11.8	24 (est.)	5.0	1.95	2.38	4.6
2 Brush Crk. Sh.	7.7	17.7	—	2.3	—	—
3 Ames Sh.	9.8	19.5	—	1.99	—	—
Sayre's 1930 measurements	7.5	14.0	2.0	1.87	3.77	7.0
Beede's 1900 measurements	7.0	14.0	1.3	2.00	4.66	9.3
Wewoka Sh. Neb. GS	9.1	18.8	4.2	2.12	2.16	4.47
Otterville specimen Neb. GS	13.1	26 (est.)	6.0	1.98	2.18	4.33

P. glabra is a common species in the Conemaugh formation and was found in the Ames and Brush Creek shales in equal numbers and in the Castleman and Georges Creek Basins. It was recovered from core holes GC 5, GC 11, GC 14, GC 15, GC 21, CB 4, CB 5, CB 6, CB 12, CB 16, CB 18, CB 22.

USNM no. 119271a,b.

Section ISODONTA
Family PTERINOPECTINIDAE
Genus DUNBARELLA Newell, 1937
DUNBARELLA APPALACHIENSIS, n.sp.
Pl. 16, figs. 21,23

Medium-size subquadrate prosocline pectinoids with three to six very faint costae on the anterior auricles. Height greater than width. Valves compressed. Umbo posterior to midpoint of hinge line. Posterodorsal angle 91°. Body costae well defined, rounded and with subequal interspaces. Costae added by intercalation on left valve and by bifurcation on right valve.

Discussion.—This species is erected on fragments of 16 left valves and two right valves plus the illustrated holotype, a slightly distorted left valve. Measurements (in mm.) of the more complete specimens are:

Specimen	Valve	Length	Height	Hinge Length	Body Costae	Costae on ant. auricle
1 (Holotype)	left	15.0	18.0	12.7	45 plus	3
2	left	8.0	—	7.3	20*	—
3	left	14.5†	—	12.7	26*	6
4 (illus.)	right	16.3	16.6	11.7	48	4

* Ventral margin missing, undoubtedly additional costae developed by intercalation.
† Estimated.

Newell (1937, p. 39) predicted that additional *Dunbarella* species would be found to bridge the gap between *D. knighti* Newell and *D. rectalaterarea* (Cox) of the Desmoinesian and *D. whitei* (Meek) of the Virgilian Stages.

D. whitei and *D. knighti* may be distinguished from the new species by the greater length in proportion to the height of the valve. *D. whitei* lacks costae on the anterior auricles and has only 24 to 32 body costae. *D. knighti* has about 78 body costae in comparison with the 45 to 48 found on *D. appalachiensis*. The only other American species having a greater height than length is *D. rectalaterarea*, which may be distinguished from *D. appalachiensis* by its 77 to 83 costae and 5 to 8 or more costae on the anterior auricle.

On the basis of the reduction of body costae and anterior auricular costae, *D. appalachiensis* would appear to represent the Missourian stage in this evolutionary line.

The holotype was found in the Georges Creek Basin in the Ames shale; the other specimens were collected from this shale, only one or two came from the Brush Creek shale. Specimens were also found in the Castleman Basin. Core holes yielding this species were: GC 2, GC 14, GC 15, GC 21, CB 4, CB 34.

The holotype is designated as USNM no. 119267a, the illustrated paratype is USNM no. 119267b. Type locality: USBM core hole 2, Georges Creek Basin, Allegany County, Maryland.

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FUSULINIDS FROM THE SUBLETT RANGE, IDAHO

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ABSTRACT—Fusulinids collected from a 1,900 foot section of Pennsylvanian-Permian rocks in the Sublett Range are illustrated and described. These indicate that the lower 750 feet of the section is of upper Pennsylvanian age and the upper 1,150 feet are of Permian Wolfcampian age. Unnamed species of *Oketaella*, *Schubertella*, and *Dunbarinella* are discussed and illustrated. One new species of *Bartramella*, *B. helgarensis*, is described. Three previously described and one unnamed form of *Triticites* are illustrated and described. One previously described species of *Pseudofusulinella*, *P. utahensis* Thompson & Bissell, is described and illustrated and several unnamed species of this genus are noted. One previously described species of *Schwagerina*, *S. wellsensis* Thompson & Hanson, and one new species. *S. sublettensis*, are described and illustrated.

INTRODUCTION AND ACKNOWLEDGMENTS

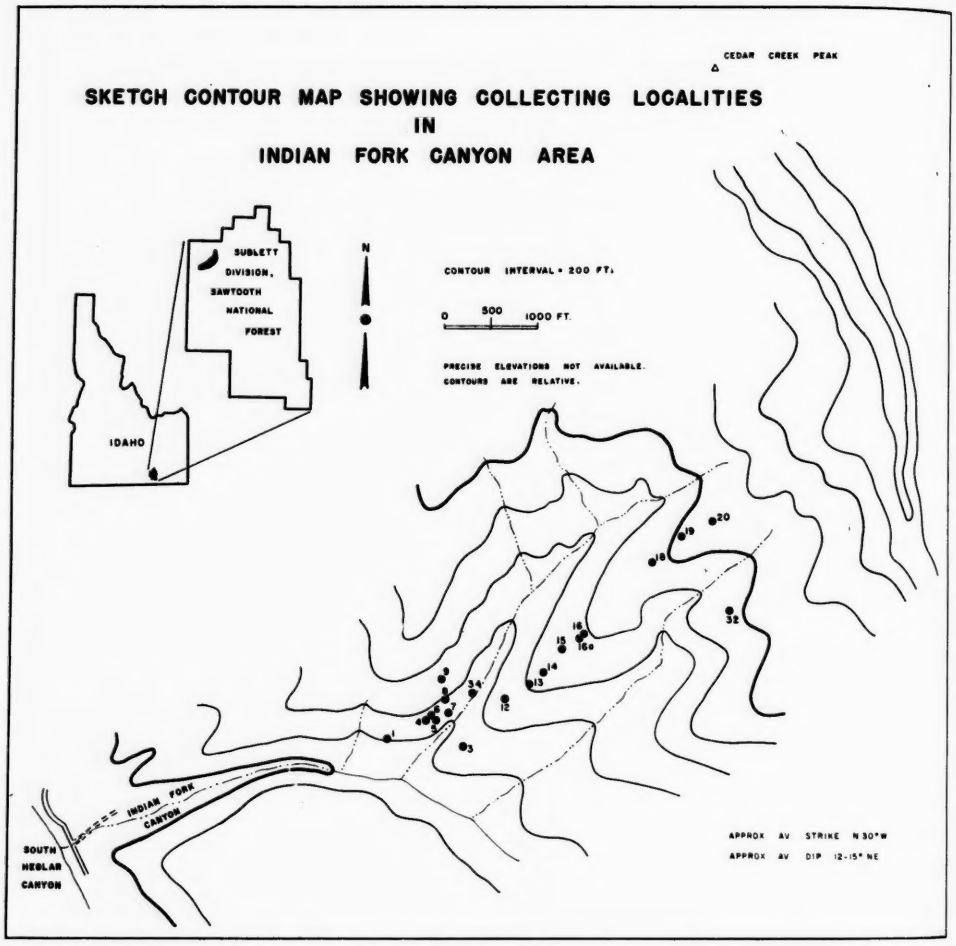
ONE of the best sequences of rocks in Idaho for collecting fusulinids is exposed in the Sublett Range. This uplift, located in the central portion of southernmost Idaho, is a north-south-trending range about 50 miles long. The greater part is in Idaho where it includes parts of Cassia, Power, and Oneida counties. The general trend of the uplift continues southward for a short distance into Boxelder County, Utah.

The oldest rocks known in the Sublett Range are 1,000 feet or more of black shale exposed in the northwestern flank of the range. Pelecypods which are either earliest Pennsylvanian or late Mississippian in age (Newell, *in* Youngquist & Haegele, 1955, p. 2080) have been collected from this shale. The bulk of the range consists of Pennsylvanian and Permian strata which are chiefly limestone and silty and sandy limestone, but also include some shales and minor other lithologies. Paleozoic strata as young as Guadalupian may be present. The youngest marine sediments are Triassic rocks preserved in a syncline along the western flank of the range in the vicinity of the Sublett Reservoir and Van Camp Creek.

The structure of the Sublett Range is complex and some thrusting is indicated (Anderson, 1931). One of the thickest and best exposed sections in the Sublett Range is in the northwestern portion beginning in Indian Fork Canyon and extending up toward Cedar Creek Peak (text-fig. 1). The basal contact of the arenaceous limestone beds (which in places are conglomeratic) with the underlying black shale is a fault contact wherever we have been able to observe it. Also, the upper portion of this Indian Fork Canyon section has been faulted, and some duplication of beds may exist. However, the lower part of this section consists of approximately 2,800 feet of strata which appear to be relatively undisturbed.

During the field season of 1950, Youngquist and Haegele made a brief survey of this area, prepared a sketch map of the topography (Text-fig. 1), and collected a number of fusulinids. Some of these were later identified by Thompson, and these identifications were included in Youngquist & Haegele's report (1955). More recently, we have had time to make and to study a large number of fusulinid thin-sections from the collections made in 1950 and these constitute the basis for the present report.

Only a few other reports on fusulinids from the Basin-and-Range Province and immediately adjacent areas have been published. Thompson, Verville, & Bissell (1950) reported on some Pennsylvanian fusulinids from the south-central Wasatch Mountain area. In his general study of Wolfcampian fusulinids in 1954, Thompson described specimens from Fusulina Peak in the Diamond Range of east-central Nevada, from a locality east of Wells, Nevada, and from the Confusion Range of western Utah. Bostwick (1955) described a number of fusulinids from the Wood River beds of south-central Idaho. Thompson & Zeller (1956) described



TEXT FIG. *1*

Profusulinella from Pennsylvanian rocks in the Conger spur of the Confusion Range in western Utah. In 1956, Knight described Permian fusulinids from the Arcturus formation and Verville, Thompson, & Lokke (1956) described Pennsylvanian specimens from the Ely limestone, all of east-central Nevada. Bostwick's paper is the only previous study of fusulinids from Idaho, and he was handicapped by the relatively poor preservation of those fossils from the Wood River formation. Because the Sublett Range contains an exceptionally thick sequence of fusulinid-bearing rocks, because the specimens are relatively well preserved, and because this area geographically forms a connecting link between the fusulinids known from the Rockies and those of the Great Basin it seems worthwhile to illustrate and describe these Sublett Range faunas. However, it should be emphasized that our fusulinid faunas probably represent only a small part of the total faunas available in the Sublett Range. The lowest fusulinid zone described here is about 900 feet above the base of the 2,800-foot section. Fusulinids are not abundant but definitely occur in the lower 900 feet of beds from which we have no satisfactory sections for illustration. Also, because of the complexity of structure, the complete Pennsylvanian-Permian section in the Sublett Range is not exposed in any one continuous sequence, and the exact thickness of the total section is difficult to ascer-

tain. The section probably can best be pieced together by means of detailed work with the fusulinid zones. It is a worthwhile area for further collecting and study.

Collecting localities are indicated in their relative positions by Text-figure 1. Each locality number represents a fusulinid-bearing rock collection made from no more than a two-foot interval. Collecting localities and collection numbers are the same. That is, Idaho collection no. 1 comes from Idaho locality no. 1.

Field work for this project was supported by the University of Idaho Special Research Project 23. Laboratory facilities and secretarial and drafting assistance were provided by the University of Kansas.

FAUNAL SUMMARY

The apparent mingling of fusulinids from several faunal provinces during Pennsylvanian times in east-central Nevada has been noted by Verville, Thompson, & Lokke (1956). This same situation seems to have existed also in the Sublett area of southern Idaho. The fusulinid fauna in the Paleozoic rocks of the Sublett Range contains representatives of the genera *Schubertella*, *Oketaella*, *Bartramella*, *Pseudofusulinella*, *Triticites*, *Dunbarinella*, and *Schwagerina*.

The genus *Schubertella* occurs widely throughout the world and has been observed in rocks of the upper Pennsylvanian and throughout the Permian. The form present in our Idaho collections described below as *Schubertella* sp. is not considered diagnostic and adds little stratigraphic information regarding the ages of the containing rocks. Specimens referable to *Schubertella* occur in our collections 1, 4, 5, 8, 13, and 34.

The genus *Oketaella* is widespread in rocks of the middle and upper Pennsylvanian and in rocks of Permian Wolfcampian age. Evolutionary trends have not been recognized among members of the genus and the forms in the Idaho collections are not considered diagnostic. Specimens of *Oketaella* are present in our Idaho collections 1, 3, 4, 5, 8, and 18. It seems that several forms are represented, but sufficient material is not present to permit a detailed specific description of any.

The genus *Bartramella* was first described from rocks of upper Desmoinesian age in eastern Nevada and has since been observed widely distributed in rocks of about the same age in New Mexico and westward into the Great Basin. The Idaho form of this genus from collection 18 described here as *B. heglarensis*, n. sp., is associated with *Schwagerina* that indicates a Wolfcampian age, and stratigraphically extends the upper limits of the genus. Common specimens of this genus are also present in our collections 3, 4, 5, 8, 13, and 14.

The genus *Pseudofusulinella* has been observed widespread in Permian rocks in the western part of Canada and the United States. It has not been found in the mid-continent area of North America. Evolutionary trends within the genus have not been determined, and its representatives so far have not been of great value for age determination. The species in our Idaho collection 20 referred to *P. utahensis* Thompson & Bissell was originally described from the Permian Wolfcampian part of the Oquirrh formation in the Wasatch Mountains of Utah. Most, if not all, previously described forms of *Profusulinella* are of Permian Wolfcampian or Leonardian age. Some of our specimens of *Profusulinella* from the Sublett Range are associated with *Triticites* that seem to be of upper Pennsylvanian Virgilian age. Evolutionary trends within the genus have not been determined. Therefore, forms of *Pseudofusulinella* in our Idaho collections do not furnish much additional information regarding ages of the rocks. However, since the species *Pseudofusulinella utahensis* is found in the Wolfcampian part of the Oquirrh formation of Utah, this suggests that in the Sublett Range the rocks from which we obtained our specimens of this form are also of Wolfcampian age. *P. utahensis* is associated in the Sublett Range with forms of the genus *Schwagerina* which further supports the conclusion that the containing rocks are of Permian age. Numerous species of *Pseudofusulinella* seem to be present in our collections, but we are describing only the one form. Our Sublett collections contain the most abundant specimens of *Pseudofusulinella* that we have observed anywhere and some of our samples are composed largely of specimens of the genus. Abundant specimens of *Pseudofusulinella* are present in our collections 1, 3, 4, 5, 8, 9, 13, 14, 15, 16, 16a, 17, 19, 20, 32, and 34.

The genus *Triticites* occurs abundantly

in our Idaho collections and seems to range in age from the Virgilian of the Pennsylvanian to Lower Permian. Those specimens of *Triticites* in collections Idaho 1 to Idaho 13 are more closely similar to Pennsylvanian Virgilian forms in the midcontinent region, and those in collection Idaho 16a are more nearly like forms commonly found in Wolfcampian rocks of other areas, such as *T. cellamagnus* Thompson & Bissell and *T. pinguis* Dunbar & Skinner. These Wolfcampian *Triticites* are associated in Idaho with forms of *Schwagerina* that seem to confirm our conclusion that they are of Wolfcampian age. Forms of *Triticites* that are similar to Pennsylvanian forms of other areas are here described as *T.* sp. A. from collection 1, *T.* cf. *T. collomensis* Dunbar & Condra from collection 7, and *T.* aff. *T. plummeri* Dunbar & Condra from collection 8. Forms of *Triticites* that seem to demonstrate Wolfcampian age for part of the Sublett rocks are here described and illustrated as *T. cellamagnus* T. & B. from collection 16a where it is associated with *Schwagerina*. Additional *Triticites* are found in collections 4, 5, 6, 9, 12, 13, and 24.

The genus *Dunbarinella* is abundant in the Virgilian of the midcontinent area and in Wolfcampian rocks of the midcontinent and Rocky Mountain region. Poorly oriented specimens of *Dunbarinella* are here illustrated from our collection 19 that resemble Wolfcampian forms of the genus from other areas.

The genus *Schwagerina* is represented in our collections Idaho 16a to Idaho 19, and demonstrates a Wolfcampian age for this part of the section. Forms referred to the genus *Schwagerina* include *S. wellsensis* Thompson & Hanson, *S. sublettensis*, n. sp., and several undescribed species.

COLLECTIONS

The following 20 samples were studied for this report. The localities from which they were obtained are indicated on Text-figure 1, and the entire fusulinid fauna observed is here listed.

1. *Pseudofusulinella* sp., *Triticites* sp. A, *Schubertella, Oketaella.*
3. *Pseudofusulinella* sp., *Bartramella* sp., *Oketaella* sp.
4. *Triticites* sp., *Pseudofusulinella* sp., *Bartramella* sp., *Schubertella* sp., *Oketaella* sp.
5. *Triticites, Bartramella, Pseudofusulinella, Schubertella, Oketaella.*
6. *Triticites* sp. cf. *T. cullomensis.*
7. *Triticites* sp. cf. *T. cullomensis, Triticites* sp.
8. *Triticites* sp. cf. *T. cullomensis, T.* sp. aff. *T. plummeri, Pseudofusulinella* sp., *Bartramella* sp., *Oketaella* sp., *Schubertella* sp.
9. *Triticites* sp. aff. *T. plummeri.*
12. *Triticites* sp. cf. *T. cullomensis, Oketaella* sp.
13. *Triticites* sp. cf. *T. cullomensis, Pseudofusulinella* sp., *Bartramella* sp., *Schubertella* sp.
14. *Pseudofusulinella* sp., *Schwagerina* sp., *Bartramella* sp.
15. *Schwagerina* sp., *Pseudofusulinella* sp.
16a. *Triticites cellamagnus, Schwagerina* sp., *Pseudofusulinella* sp.
16. *Pseudofusulinella* sp., *Schwagerina* sp., *Triticites* sp.
17. *Schwagerina* sp., *Bartramella* sp.
18. *Schwagerina wellsensis, S. sublettensis*, n. sp., *Bartramella heglarensis*, n. sp., *Oketaella* sp.
19. *Schwagerina wellsensis, Pseudofusulinella* sp., *Dunbarinella* sp.
20. *Pseudofusulinella utahensis, Schwagerina* sp.
32. *Pseudofusulinella* sp.
34. *Pseudofusulinella, Schubertella* sp., *Triticites* sp. cf. *T. cullomensis.*

SYSTEMATIC PALEONTOLOGY

SCHUBERTELLA sp.

Pl. 17, figs. 1–4

Specimens referable to the genus *Schubertella* have been observed in several of our collections from the Sublett Range, including Idaho 1, 4, 5, 8, and 13. The better preserved of these are from collection Idaho 4, obtained from the northwest side of the canyon north of Indiana Falls. The larger of these specimens has an asymmetrical discoidal shell of one to two volutions and four outer fusiform volutions that coil uniformly and that attain a length of 1.4 mm. and a width of 0.5 mm. The chomata are small but are highly asymmetrical. The septa are inflated throughout all parts of the shell.

The form in collection Idaho 4 resembles in some respects *Schubertella kingi* Dunbar & Condra of wide distribution in lower Wolfcampian rocks but differs from that form by its thicker shell, more inflated shell, and considerably larger shell.

The illustrated specimens are from collections 4 and 8.

OKETAELLA spp.

Pl. 17, figs. 5–10

Specimens referable to the genus *Oketaella* have been observed in many of the collections from the Sublett Range including

Idaho 1, 3, 4, 5, 8, and 18, a few of which are illustrated on the accompanying plates. In no case do we feel that we have sufficient material for detailed description. It is evident that a number of species are represented by these specimens that range in age from Pennsylvanian where they are associated with Virgilian *Triticites* and *Bartramella* to Wolfcampian where they are associated with *Bartramella* and *Schwagerina*.

The illustrated specimens are from collections 4, 8, and 12.

BARTRAMELLA HEGLARENSIS, n. sp.
Pl. 17, figs. 11–14

The shell of *Bartramella heglarensis*, n. sp., is small and elongate fusiform; with a curved or irregular axis of coiling. The lateral slopes are convex throughout the inner four volutions and are concave in the outer more extended volutions. The polar ends are sharply pointed in the inner volutions, with the exception of the first, and are bluntly pointed in the outer volutions. The profile of the first volution is subcircular to elliptical in shape and that of successive volutions progressively become more elongate fusiform in shape. Larger shells of eight volutions are 4.3 to 5.7 mm. long and 1.3 to 1.5 mm. wide, giving form ratios of 3.1 to 4.3. Averages of the form ratios of the first to the eighth volution of five specimens are 1.5, 2.3, 2.5, 3.1, 3.5, 3.5, 3.3, and 3.6, respectively.

The proloculus is small and spherical to elliptical in shape and has an outside diameter to 70 to 93 microns, averaging 83 microns in five specimens. Chambers increase in height slowly but uniformly, with average height of chambers for the first to eighth volution in five specimens of 27, 38, 51, 63, 87, 113, 138, and 157 microns, respectively. The chambers are lowest above the tunnel, and they increase in height slightly toward the poles.

The structure of the spirotheca is not distinct in most specimens, but some specimens show a very thin dark tectum and an inner thicker clearer layer. The spirotheca thins slowly toward the poles in most of the specimens studied. However, this thinning is not apparent in some specimens, and the spirotheca seems to be of equal thickness throughout the length of the shell. Averages

TABLE 1—MEASUREMENTS OF *Bartramella heglarensis* N. SP., IN MILLIMETERS (IDAHO 18). SPECIMEN 3 IS THE HOLOTYPE

Specimen	L.	W.	Ratio	No. Vol.	Diam. of prol.	Height of volutions							
						1	2	3	4	5	6	7	8
1	5.0	1.5	3.1	8	.083	.022	.037	.051	.064	.093	.120	.140	—
2	5.0	1.4	3.5	8	.093	.027	.046	.048	.054	.086	.106	.135	.166
3	6.0	1.3	4.3	8	.093	.032	.034	.055	.056	.086	.093	.155	.127
4	4.3	1.3	3.3	8	.070	—	.038	.048	.060	.087	.118?	.120?	.179
5	4.0	1.0	4.0	6½	.078	.026	.035	.055	.082	.082	.129	—	—

Specimen	Form ratio of volutions								Thickness of spirotheca							
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1	1.7	2.7	2.8	3.0	3.9	3.3	3.2	3.1	.004	.006	.010	.014	.022	.022	.046	—
2	1.4	2.2	2.4	2.7	4.2	3.3	3.7	3.5	.003	.009?	.010	.009	.022	.023	.043	.033
3	1.6	2.4	2.2	3.1	3.4	3.8	3.5	4.3	.004	.010	.011	.012	.016	.035	.035	.035
4	1.7	2.4	2.6	3.3	3.2	3.2	2.9	3.3	—	.006	.012	.017	.015	—	.028	.038
5	1.2	1.6	2.5	3.2	2.8	3.8	—	—	.004	.009	.010	.019	.020	.020	—	—

Specimen	Tunnel angle (degrees)							
	1	2	3	4	5	6	7	8
1	—	—	—	17	20	20	31	28
2	—	—	15	14	20	25	29	29
3	—	—	18	20	22	23	23	24
4	—	—	—	25	30	30	30	—
5	—	—	21	20	19	27	—	—

of the thicknesses of the spirotheca above the tunnel in the first to the eighth volution of five specimens are 4, 8, 11, 14, 19, 20, 38, and 35 microns, respectively. The proloculus wall averages about 5 microns in thickness for five specimens.

The septa are fluted throughout the length of the shell. The fluting is narrow and extends to or near the top of the chambers for the entire length of the shell. No sagittal section of this form was obtained.

The tunnel path is well defined, narrow, and irregular. Averages of the tunnel angles in the third to the eighth volution in five specimens are 18, 19, 22, 25, 28, and 27 degrees, respectively. The chomata are relatively large in the inner four or five volutions where they are highly asymmetrical and are generally more massive and are symmetrical but small in outer volutions. In the inner four or five volutions the chomata deposits extend laterally to join with dense axial fillings. The inner three or four volutions are almost completely filled with axial fillings which are extremely massive in the polar region and are thinner toward the center of the shell. In the outer volutions the axial fillings are limited to dense deposits in the polar regions.

Discussion.—Only one other species, the type species, of the genus *Bartramella* has been reported previously from North America. This species, *Bartramella bartrami* Verville, Thompson, & Lokke, is from the Ely limestone in the Cherry Creek Mountains of White Pine County, Nevada. *Bartramella bartrami* is associated with *Fusulinella alta* Verville, Thompson, & Lokke, and *Fusulina weintzi* Verville, Thompson, & Lokke.

Bartramella heglarensis is similar to *B. bartrami*, but differs from it in several respects. *B. heglarensis* has a thicker spirotheca especially in the outer volutions, has a distinctly narrower tunnel, has axial fillings that are more extensive and spread nearer to the center of the shell in the inner volutions, and has a larger shell. These differences seem to indicate a trend in the genus *Bartramella* toward increase in shell size and spirothecal thickness from the middle Pennsylvanian to the Wolfcampian. However, stratigraphically intermediate species must be studied before a definite trend or trends can be established.

Occurrence.—*Bartramella heglarensis* is abundant in the Sublett collection 18, where it is associated with *Schwagerina sublettensis*, n. sp., and *S. wellsensis* Thompson & Hanson. Other specimens assigned to the genus *Bartramella* are in collections Idaho 3, 4, 5, 8, and 13, where they are associated with Virgilian *Triticites*. Other specimens of *Bartramella* are present in collection 17. The specific name is derived from South Heglar Canyon to which Indian Fork Canyon (containing these fusulinid localities) is tributary.

PSEUDOFUSULINELLA UTAHENSIS
Thompson & Bissell, 1954
Pl. 18, figs. 1–8

Pseudofusulinella utahensis THOMPSON & BISSELL, 1954, Univ. Kans. Paleont. Contr., Protozoa, Art. 5, p. 34, 35, pl. 7, figs. 1–10.

The shell of *Pseudofusulinella utahensis* Thompson & Bissell is small and elongate fusiform; with an irregular axis of coiling, pronounced extension of the polar ends in the outer volutions, an inflated central region, and straight to concave lateral slopes. Shells of seven to nine volutions average 4.3 mm. in length and 1.7 mm. in width, giving an average form ratio of 2.5. The first volution has a short axis of coiling and is ellipsoidal to subspherical in shape, the axial ends become elongated with a corresponding inflation of the central region in successive volutions. Averages of the form

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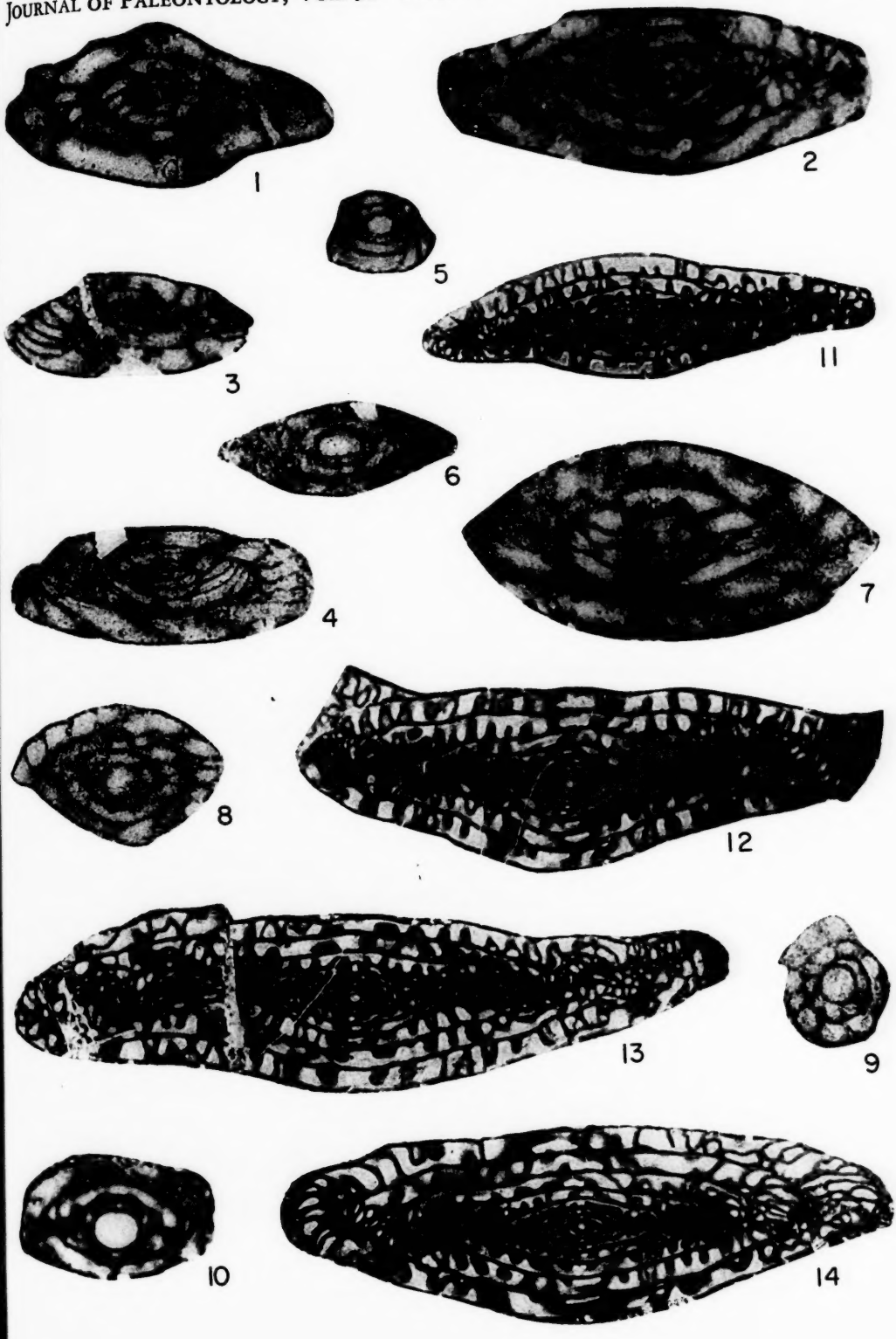
EXPLANATION OF PLATE 17

All illustrations on this plate are unretouched photographs and all of them are magnified ×50 except *11* to *14* which are magnified ×20.

FIGS. *1–4—Schubertella* sp. *1,4*, Tangential sections; *2,3*, axial sections. All from Idaho 4.

5–10—Oketaella spp. *5,6,8,10*, Axial sections; *7*, tangential section; and *9*, sagittal section. *5* is from Idaho 12, *6,7*, and *8* are from Idaho 8, and *9* and *10* are from Idaho 4.

11–14—Bartramella heglarensis T. D. & Y., n. sp. All axial sections from Idaho 18.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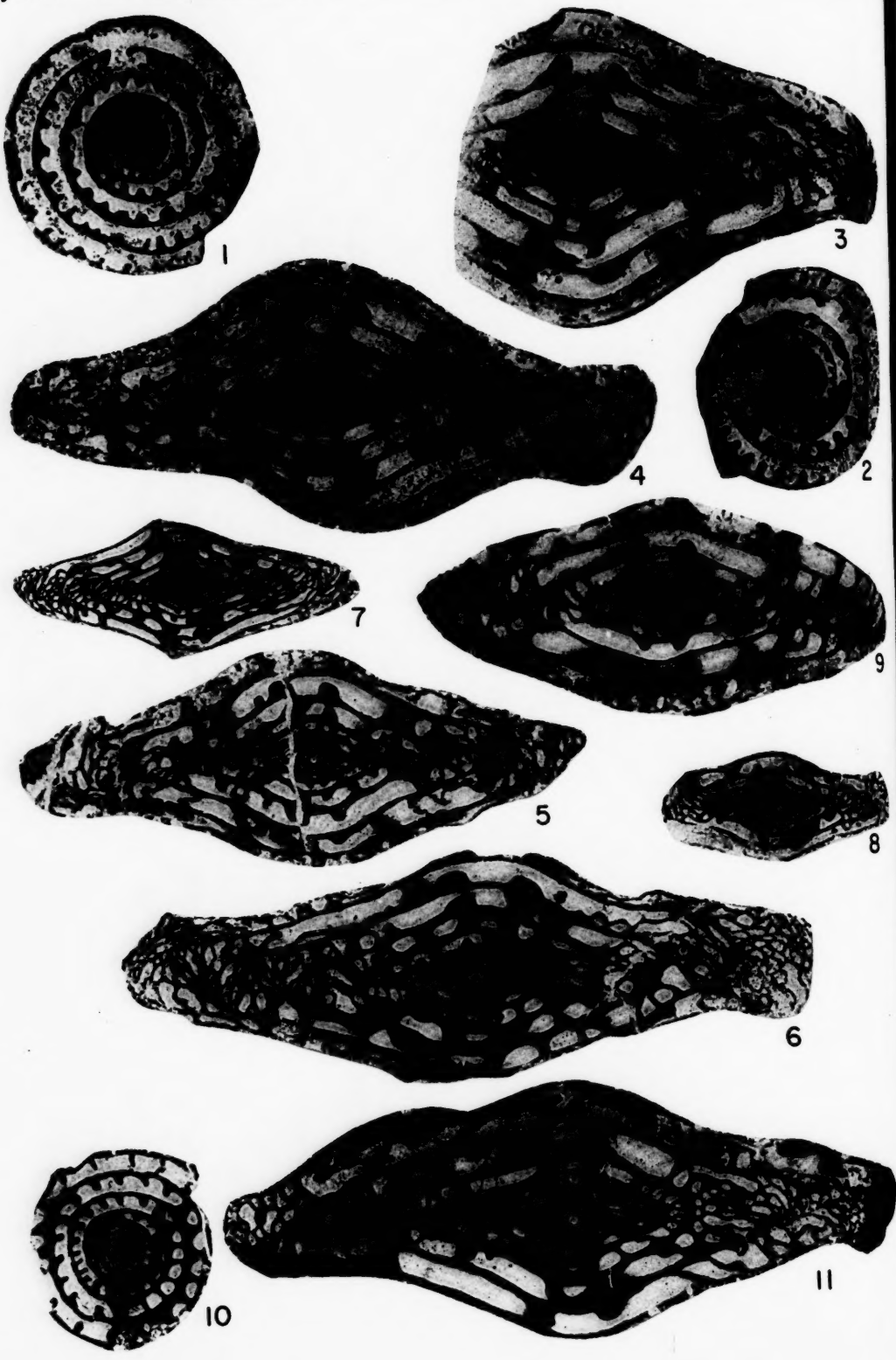
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ratios of the first to ninth volution of eight specimens are 1.6, 2.0, 2.3, 2.3, 2.3, 2.4, 2.6, 2.2, and 2.4, respectively.

The proloculus is small and spherical or elliptical in shape, with its outside diameter of 63 to 107 microns and averaging 80 microns for eleven specimens. In the more inflated specimens the chambers are highest above the tunnel, and the chamber height decreases toward the poles and increases again at the polar ends. Less inflated forms show about equal chamber height throughout, with perhaps a slight increase toward the poles.

The thin spirotheca is composed of a distinct tectum and a lower clearer layer of an indistinctly porous nature. Average thicknesses of the two layered spirothecal wall in the first to eighth volution of eleven specimens are 6, 5, 11, 18, 23, 27, 27, 38, and 34 microns, respectively.

The septa are composed of a downward deflection of the tectum and the lower clear layer. In most specimens it is difficult to see the deflected nature of the tectum, and the septa appear to be composed of a downward deflection of only the lower clear layer. The septa are moderately fluted in the polar region and relatively unfluted across the central part of the shell. Average septal counts of the first to seventh volution of three specimens are 8, 13, 16, 17, 18, 21, and 25, respectively.

The tunnel is narrow in the inner volutions and widens in the outer volutions. The average tunnel angles in the third to eighth volution of eight specimens are 16, 19, 21, 23, 26 and 26 degrees, respectively. The chomata are massive and asymmetrical, with steep to overhanging tunnel margins and moderate to steep polar sides. The chomata extend from one-half to two-thirds the height of the chambers in the center of the chambers. Where in contact with septa, they extend to the top of the chambers. The chomata extend laterally as irregular deposits on the spirotheca.

Discussion.—The specimens of *P. utahensis* from the Sublett collections are similar to those described from the Oquirrh formation in the southern part of the Wasatch Mountains near Provo, Utah. The average spirothecal thickness in the Sublett specimens is slightly greater in the outer five volutions, the height of their chambers is definitely less in the outer five volutions, and the tunnel angles are smaller in the outer few volutions. All other measurable features of the two sets of specimens are almost identical.

Pseudofusulinella utahensis resembles *Neofusulinella* sp. described by Thompson & Verville (1950) from the Permian rocks of Kamloops, B. C., Canada. *P. utahensis* differs from this Canadian form by its smaller size, more inflated shell, and lighter axial fillings.

Occurrence.—*Pseudofusulinella utahensis* is found in collections Idaho 16, 17, 19, and 20. It has been reported from about 11,700 feet above the base of the Wood River formation, near Bellevue, Idaho, and was originally described from the upper Oquirrh formation of Utah. All indications point to a Wolfcampian age for this species. *P. utahensis* is associated with *Schwagerina wellsensis, Schwagerina* sp., and *Dunbarinella?*. Two unanamed species of *Pseudofusulinella* are here illustrated from collection 3 (Pl. 4, fig. 1; Pl. 2, fig. 9) and collection 32 (Pl. 2, fig. 10, 11) that differ from *P. utahensis* in several respects. These latter two forms are considered to be of Pennsylvanian age. Numerous other forms of the genus are present in our collections of both Pennsylvanian and Permian ages.

EXPLANATION OF PLATE 18

All illustrations on this plate are unretouched photographs and all are magnified ×20 except *7* and *8* which are ×10.

FIGS. *1–8—Pseudofusulinella utahensis* Thompson & Bissell. *1,2*, Sagittal sections; and *3–8*, axial sections. All from Idaho 20.

9—Pseudofusulinella sp. Axial section from Idaho 3.

10,11—Pseudofusulinella sp. *10*, Sagittal section; and *11*, axial section. Both from Idaho 32.

TRITICITES sp. cf. T. CULLOMENSIS Dunbar & Condra
Pl. 19, figs. 3–6,8

Triticites cullomensis DUNBAR & CONDRA (part), 1928, Nebr. Geol. Survey Bull. 2, 2nd Ser., p. 93–95, pl. 5, figs. 6,7,9 (1927) (*Not* figs. 5,8,10). WHITE, 1932, Tex. Univ. Bull. 3211, p. 43, 44, pl. 3, figs. 1–3. DUNBAR & HENBEST, 1942, Ill. Geol. Survey Bull. 67, p. 135, 136, pl. 23, figs. 13–18. THOMPSON, VERVILLE, & BISSELL, 1950, Jour. Paleontology, v. 24, no. 4, p. 457–460, pl. 62, figs. 7–17, pl. 63, figs. 1–3.

The shell of *Triticites* sp. cf. *T. cullomensis* Dunbar & Condra is of medium size, short inflated fusiform in shape, has bluntly pointed to rounded polar ends and uniformly convex lateral slopes. Specimens of six and a half to seven and a half volutions are 5.4 to 6.4 mm. long and 2.2 to 2.6 mm. wide. Averages of the form ratios for the first to seventh volution of four specimens are 1.5, 2.1, 2.1, 2.3, 2.6, 2.4, and 2.3, respectively.

The proloculus is medium to small in size, measuring from 102 to 142 microns in outside diameter and averaging 123 microns for four specimens. The chambers are uniform in height from above the tunnel to the polar ends. Averages of the chamber height for the first to seventh volution of four specimens are 47, 64, 122, 186, 253, 324, and 337 microns, respectively. The 337 micron height for the seventh volution is based on only one specimen.

The spirotheca is composed of a tectum and a medium to coarsely alveolar keriotheca. Averages of the thickness of the spirotheca for the first to the seventh volution of four specimens are 12, 19, 29, 48, 73, 89, and 74 microns, respectively. The thickness of the proloculus wall averaged 15 microns in four specimens.

No sagittal section of this form was obtained. In axial thin sections the septa are seen to be closely fluted in the polar regions with little or no fluting present in the central regions.

The tunnel is straight and tunnel angles average 28, 32, 35, 30, and 35 degrees, respectively, for the third to seventh volution of four specimens. The chomata deposits are fairly well developed in the second to fifth volution, with their maximum thickness being about one-half the height of the chamber. The chomata are rounded-rectangular or semi-elliptical in cross section and nearly symmetrical in design. In the first through fourth volution the chomata extend laterally into thin irregular deposits which continue for a short distance toward the poles

TABLE 2.—MEASUREMENTS OF *Triticites* CF. *T. Cullomensis* DUNBAR & CONDRA (SUBLETT NO. 7) IN MILLIMETERS

Specimen	L.	W.	Ratio	No. Vol.	Diam. of prol.	Height of volutions						
						1	2	3	4	5	6	7
1	5.4	2.6	2.1	7½	.102	.046	.058	.111	.177	.193	.337	.337
2	6.4	2.2	2.8	6½	.126	.048	.077	.139	.179	.279	.310	—
3	6.3	2.3	2.7	6½	.142	.051	.058	.120	.191	.220	.325	—
4	4.8	2.0	2.4	5½	.121	.044	.062	.114	.198	.321	—	—

Specimen	Form ratios of volutions						
	1	2	3	4	5	6	7
1	1.1	1.6	1.7	2.0	2.1	2.1	2.3
2	1.7	2.4	2.0	2.3	2.5	2.4	—
3	1.7	1.9	2.1	2.0	3.0	2.7	—
4	1.3	2.4	2.6	2.7	2.7	—	—

Specimen	Thickness of spirotheca							Tunnel angle (degrees)						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
1	.015	.016	.021	.051	.053	.120	.074	—	—	25	30	27	30	35
2	.011	.026	.031	.045	.074	.080	—	—	—	28	26	32	—	—
3	.010	.020	.035	.062	.080	.084	—	—	—	34	36	41	—	—
4	.010	.015	.024	.046	.067	—	—	—	—	25	36	39	—	—

In most specimens these extensions are not discernible in the fifth volution.

Discussion.—The specimens here described as *Triticites* cf. *T. cullomensis* are similar to those described by Thompson, Verville, & Bissell (1950) from the Oquirrh formation of south-central Wasatch Mountains of Utah. However, close comparison reveals the following differences. The Sublett specimens have thicker spirotheca, and the height of volutions is greater. The description of the Sublett form is based on fewer specimens than that described from the Oquirrh formation. *Triticites cullomensis* from the Sublett Mountains is smaller and has a thinner spirotheca than the type specimen from the midcontinent. The rocks in which these specimens occur are Virgilian in age and correlate with the Shawnee group of the midcontinent region.

Occurrence.—*Triticites* cf. *T. cullomensis* is abundant in Sublett collection no. 7 where it is associated with *Triticites* aff. *T. hobblensis* Thompson (pl. 4, fig. 7) and *Triticites* sp.

Species of *Triticites* similar to *T. cullomensis* have been reported very widespread in America from the upper 1,200 feet of the Oquirrh formation of the south-central Wasatch Mountains in Utah, from 1,300 to 4,850 feet above the base of the Wood River formation near Bellevue, Idaho, from the Beil limestone of Kansas, the Ames limestone at Brilliant Cut, Pittsburgh, Pennsylvania, and from the Jackboro limestone member of the Caddo Creek formation, Jack County, Texas. Specimens of *Triticites* of this general type are typical of rocks of about the same age as the Shawnee group of Kansas. In the Sublett Range, specimens of this general type are abundant in our collections 6, 7, 8, 12, and 13. The illustrated specimens are from Idaho collection 7 where they are associated with several more highly inflated specimens (Pl. 19, fig. 7). All measured specimens are from collection 7.

TRITICITES sp. aff. T. PLUMMERI Dunbar & Condra
Pl. 19, figs. 9–12

Triticites plummeri DUNBAR & CONDRA, 1928, Nebr. Geol. Survey Bull. 2, ser. 2, p. 98,99, pl. 6, figs. 1–6.

Highly inflated specimens of *Triticites* that have a minute proloculus and that resemble *T. plummeri* in some respects are abundant in collection 8 from only a short distance above collection 7. The spirotheca of this form increases in thickness rapidly with growth of the shell and indicates that this part of the section is equivalent in age to middle Virgilian.

All of our specimens of this form are from collection 8 where they are associated with specimens here referred to as *T.* cf. *T. cullomensis*, *Pseudofusulinella* sp., *Bartramella* sp., *Oketaella* sp., and *Schubertella* sp.

TRITICITES CELLAMAGNUS Thompson & Bissell
Pl. 19, figs. 13–15

Triticites cellamagnus THOMPSON & BISSELL, 1954, Univ. Kans. Paleont. Contr., Protozoa, Art. 5, p. 43–44, pl. 10, figs. 14–17, pl. 11, figs. 1–12.

We obtained several specimens of a large *Triticites* in collection 16a that are very closely similar to the type specimens of *T. cellamagnus*, originally described from the Oquirrh formation in the Wasatch Mountains of Utah. Our specimens attain a thickness as great as 4.5 mm. and a length of near 6.8. They have a large irregular proloculus and have a spirotheca that becomes abnormally thick in outer volutions. They compare favorably with the type specimen of *T. cellamagnus* but also resemble the type specimen of *T. pinguis* Dunbar & Skinner from the type section of the Wolfcampian. They are associated in our Idaho collection with forms of *Schwagerina* and *Pseudofusulinella*.

TRITICITES sp. A
Pl. 19, figs. 1,2

Two thin sections of a small *Triticites* are present in our collection 1 that are composed of five volutions and are about 2.0 mm. long and 1.2 mm. wide. They are associated with abundant *Pseudofusulinella*, a form of *Schubertella*, and a species of *Oketaella*. This form differs from other *Triticites* of our collection by its minute size.

In general size and shape, this species resembles somewhat closely *Triticites pygmaeus* Dunbar & Condra from the Missourian of Nebraska. However, its wall is relatively thicker. This form may be of Missourian age.

SCHWAGERINA WELLSENSIS Thompson & Hanson, 1954
Pl. 20, figs. 9–14

Schwagerina wellsensis THOMPSON & HANSON, 1954, Kans. Univ. Paleont. Contr., Protozoa, Art. 5, p. 64, pl. 32, figs. 1–6, pl. 34, figs. 1–12.

The shell of *Schwagerina wellsensis* Thompson & Hanson is large, inflated fusiform; with a slightly irregular axis of coiling, pointed poles and convex lateral slopes. Specimens of five to six volutions are 6.5 to 8.5 mm. long and 1.9 to 3.1 mm. wide, with resulting form ratios of 2.7 to 2.8. The first volution is elliptical to fusiform in shape with successive volutions becoming elongate fusiform. Average form ratios of the first to sixth volution in five specimens are 1.6, 2.1, 2.2, 2.4, 2.6, and 2.8, respectively.

The proloculus is large, with the outside diameter of different specimens measuring 200 to 327 microns, with an average of 263 microns for five specimens. The shell is loosely coiled with a slow and regular rate of expansion. The chambers are uniform in height throughout the central one-half to two-thirds of the shell and are slightly higher at the polar ends. The average height of the chambers above the tunnel in the first to sixth volution in five specimens is 96, 137, 202, 296, 324, and 279 microns, respectively. The height of the sixth volution is questionable as only one crushed specimen was measured. Undulations in the spirotheca along the lateral slopes are quite noticeable and produce slight irregularity in the height of chambers as seen in an axial section.

The thick coarsely alveolar spirotheca is distinct in all specimens studied. The spirotheca is thickest in the tunnel area and is irregularly thinner toward the poles. The average thickness of the spirotheca in the first to sixth volution in five specimens is 22, 36, 66, 87, 104, and 90 microns, respectively. The 90 micron thickness measured for the sixth volution is based on one measured section. The thickness of the proloculus wall averaged 22 microns for five specimens.

The septa are highly fluted and closely spaced throughout the shell. The fluting extends to the top of the chambers throughout the shell and brings the septa in contact with each other for one-third to two-thirds of their height. The septal counts of the first to fourth volution in one specimen are 10, 16, 22, and 26, respectively.

The tunnel is narrow in the second volution to moderately wide in the fifth volution. The sides of the tunnel are masked by the intense fluting which continues to the tunnel sides in all volutions. The tunnel angle averages in the second to fifth volution for four specimens are 26, 31, 33, and 42 degrees, respectively. The chomata deposits are generally small and irregulary developed. The chomata range from one-half the height of a volution to complete absence. Chomata are not present in the outer volution of most specimens studied. Light to relatively heavy axial fillings are present in all volutions with the exception of the outermost volution.

Discussion.—The Sublett specimens of *Schwagerina wellsensis* differ slightly from the original type found near Wells, Nevada, in that they are slightly more inflated.

Occurrence.—*Schwagerina wellsensis* is abundant in the collection from Sublett locality No. 19 and is rare in No. 18. It is associated in No. 19 with *Pseudofusulinella utahensis* Thompson & Bissell, *Dunbarinella?*, and *Schwagerina* sp.

EXPLANATION OF PLATE 19

All illustrations on this plate are unretouched photographs and all are magnified ×10 except *1* and *2* which are magnified ×20.

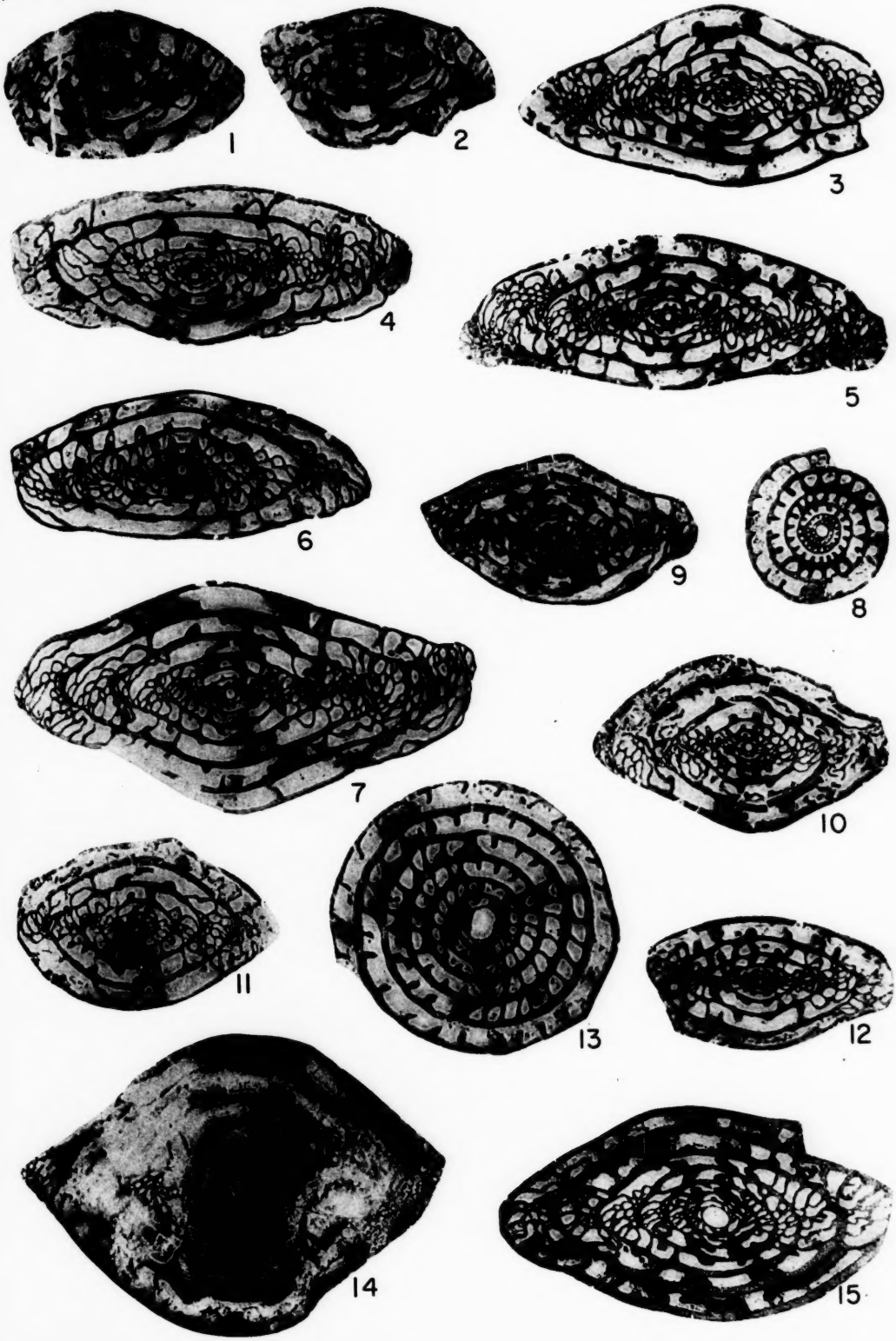
FIGS. *1,2—Triticites* sp. A. Axial sections from Idaho 1.

3–6,8—Triticites cf. *T. cullomensis* Dunbar & Condra. *3–6*, Axial sections; *8*, sagittal section. All from Idaho 7.

7—Triticites sp. Axial section from Idaho 7.

9–12—Triticites cf. *T. plummeri* Dunbar & Condra. All axial sections. *9–11*, from Idaho 8; *12* from Idaho 9.

13–15—Triticites cellamagnus Thompson & Bissell. *13*, Sagittal section; and *14,15*, axial sections. axial sections. All from Idaho 16a.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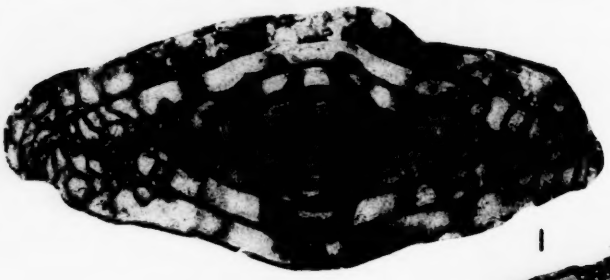

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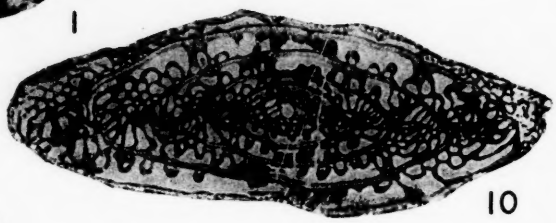

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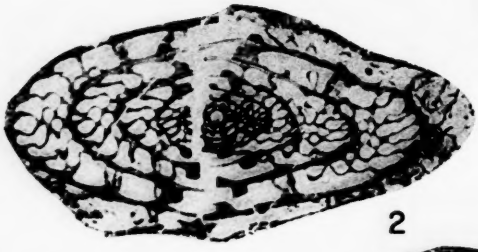

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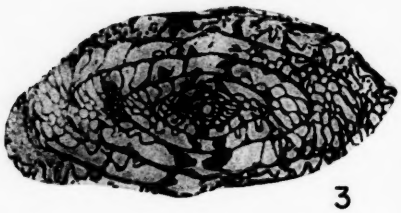

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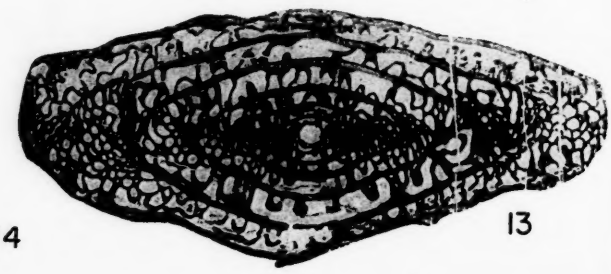

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TABLE 3—MEASUREMENTS OF *Schwagerina wellsensis* THOMPSON & HANSON (IDAHO 19) IN MILLIMETERS

Specimen	L.	W.	Ratio	No. Vol.	Diam. of prol.	Height of volutions					
						1	2	3	4	5	6
1	8.6	3.1	2.8	6	.327	.097	.155	.234	.339	.334?	—
2	5.3	2.0	2.7	5	.238	.117	.126	.159	.270	.309?	—
3	—	2.3	—	5½	.200?	.072	.121	.126	.215	.329	.279
4	6.6	2.5	2.7	5	.321	.098	.148?	.279?	.418	—	—
5	5.5	1.7	3.3	4½	.229	.194	.133	.213	.286	—	—

Specimen	Form ratio of volutions						Thickness of spirotheca					
	1	2	3	4	5	6	1	2	3	4	5	6
1	1.8	2.2	2.3	2.3	2.4	2.8?	.024	.033	.062	.110	.090	—
2	1.7	2.1	2.1	2.5	2.7	—	.020	.037	.067	.086	.117	—
3	1.7	2.3	2.3	2.2	2.7	—	.019	—	.044	.066	.093	.090
4	1.3	1.7	2.2	2.6	—	—	.023	.037	.074	.087	.116?	—
5	—	—	—	—	—	—	.026	.035	.082	.087	—	—

Specimen	Septal Count				Tunnel angle (degrees)				
	1	2	3	4	1	2	3	4	5
1	—	—	—	—	—	24	—	30	—
2	—	—	—	—	—	26	31	31	38
3	10	16	22	26	—	—	—	—	—
4	—	—	—	—	—	29	31	33	—
5	—	—	—	—	—	—	30	37	45

SCHWAGERINA SUBLETTENSIS, n. sp.
Pl. 20, figs. 4–8

The shell of *Schwagerina sublettensis*, n. sp., is elongate fusiform in shape; with a straight to slightly curved axis of coiling, sharp to bluntly pointed poles and convex lateral slopes. Specimens of five to six and a half volutions are 3.5 to 6.4 mm. long and 1.5 to 1.9 mm. wide, giving form ratios of 2.4 to 3.3. The first volution is subcircular to elliptical in profile, the second is elliptical, and successive volutions are increasingly elongate fusiform in shape. Average form ratios of the first to sixth volution of five specimens are 1.4, 1.7, 2.2, 2.3, 2.6, and 3.1, respectively.

The proloculus is small, with the outside diameter measuring 102 to 165 mircons and averaging 142 microns for seven specimens. The shell expands slowly and uniformly. The chambers are lowest above the tunnel and are higher toward the polar ends. Average height of the chambers above the tunnel in the first to seventh volution of seven specimens is 43, 65, 107, 164, 215, 257, and 258 microns, respectively.

The spirotheca is moderately thick and coarsely alveolar. The average spirotheca

EXPLANATION OF PLATE 20

All illustrations on this plate are unretouched photographs and all of them are magnified ×10, except *1* which is magnified ×20.

FIG. *1—Pseudofusulinella* sp. Axial section from Idaho 3.

2,3—Dunbarinella sp. Oblique sections from Idaho 19.

4–8—Schwagerina sublettensis T, D, & Y, n. sp. *4–7*, Axial sections; and *8*, sagittal section. *4,6,7*, and *8* are from Idaho 18 and *5* is from Idaho 19.

9–14—Schwagerina wellsensis T & H. *9*, Sagittal section; and *10–14*, axial sections. All from Idaho 19.

TABLE 4—MEASUREMENTS OF *Schwagerina sublettensis*, N. SP. (SUBLETT NO. 18)
SPECIMEN 1 IS THE HOLOTYPE

Specimen	L.	W.	Ratio	No. Vol.	Diam. of prol.	Height of volutions						
						1	2	3	4	5	6	7
1	6.4	1.9	3.3	6	.165	.053	.071	.138	.186	.220	—	—
2	5.4	1.7	3.2	6½	.144	.048	.060	.109	.166	.196	—	—
3	3.6	1.5	2.4	5	.158	.042	.069	.126	.155	.219	—	—
4	2.7	1.1	2.5	4½	.163	.051	.073	.103	.153	.186	—	—
5	4.7	1.7	2.8	5	.156	.046	.077	.111	.201	.290?	—	—
6	—	1.8	—	6	.105	.035	.063	.111?	.161?	.231	.267	—
7	—	1.8	—	6½	.102	.028	.045	.074	.129	.162	.246	.258

Specimen	Form ratio of volutions						Thickness of spirotheca						
	1	2	3	4	5	6	1	2	3	4	5	6	7
1	1.6	1.8	2.3	2.5	2.7	3.3	.012	.040	.044	.079	.113	.073?	—
2	1.1	1.7	1.9	2.0	2.5	2.8	.008	.017	.033	.067	.062	.108	—
3	1.4	1.7	2.1	2.1	2.4	—	.010	.023	.046	.057	.078?	—	—
4	1.3	1.6	2.0	2.0	—	—	.012	.017	.035	.057	.080	—	—
5	1.4	1.8	2.5	2.7	2.8	—	.009	.022	.035	.080	.110	—	—
6	—	—	—	—	—	—	.007	.015	.030	.046	.078	.108	—
7	—	—	—	—	—	—	.006	.011	.020	.040	.051	.088	.093

Specimen	Septal Count						Tunnel angle (degrees)				
	1	2	3	4	5	6	1	2	3	4	5
1	—	—	—	—	—	—	—	—	—	—	—
2	—	—	—	—	—	—	—	—	29	27	40
3	—	—	—	—	—	—	—	24	26	29	35
4	—	—	—	—	—	—	—	26	32	33	—
5	—	—	—	—	—	—	—	25	29	36	—
6	10	15	20	22	25	28	—	—	—	—	—
7	10	14	16	21	26	27	—	—	—	—	—

thickness in the first to seventh volution of seven specimens is 9, 21, 35, 61, 82, 94, and 93 microns, respectively. The spirotheca is the same thickness within the central one-half to two-thirds of each volution and is thinner poleward. The thin proloculus wall averages 12 microns for the seven specimens measured.

The fluting is narrow and fairly widely spaced throughout the shell. It extends to the tops of the chambers in the axial portions of the shell, but averages about two-thirds the chamber height in the central third of the shell. The fluting brings the septa in contact with each other for between one-half and two-thirds of their height. The septa are composed of wedges of pycnotheca which thicken toward their base. Septal counts of the first to sixth volution in two specimens average 10, 15, 18, 22, 26, and 28, respectively.

The tunnel is narrow in the second volution and becomes regularly wider in each volution up to the fifth volution. The average tunnel angles of the second to fifth volution in four specimens are 25, 29, 31, and 28 degrees, respectively. The chomata deposits are quite distinct within the inner volutions, but are irregular in their development and masked by adjacent fluting in the outer volutions. Chomata deposits are noticeably absent in the outer volution of all specimens and are generally lacking or poorly developed in the penultimate volution. Axial fillings are seen in the axial portion of the inner volutions in some specimens.

Discussion.—Schwagerina sublettensis is somewhat similar to *S. emaciata* (Beede). However, it differs from this latter form in several respects. In *S. sublettensis* the average proloculus size is larger, the form ratio

for each volution demonstrates a more inflated nature, the height of corresponding volutions is less especially in the outer volutions, and the spirothecal thickness is greater in all volutions except the first.

Schwagerina sublettensis might be confused with *S. providens* Thompson & Hazzard. However, *S. sublettensis* is smaller, has a much smaller proloculus, has lower volutions throughout the shell, usually has a thicker spirotheca, and has light axial fillings.

This species is associated with *Bartramella heglarensis*, n. sp., and *Schwagerina wellsensis*.

Occurrence.—This species is found in our Idaho 18 collection.

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FENESTRATE BRYOZOA IN THE CHOUTEAU GROUP OF CENTRAL MISSOURI

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ABSTRACT—Four new species of *Fenestella*—*F. alternata, F. aequalis, F. oblongata, F. rotundata*—and one new species of *Ptiloporella*—*P. varia*—are described from the Mississippian Chouteau group of central Missouri. Four previously described species of *Fenestella*—*F. regalis* Ulrich, *F. rudis* Ulrich, *F. serratula* Ulrich, *F. parallela* Hall—one species of *Ptiloporella*—*P. inaequalis* (Hall and Simpson)—and an undesignated species of *Ptylopora* from the same group are discussed and illustrated.

INTRODUCTION

THE considerable volume of paleontological work that has been done in the past on the fauna of the Chouteau group shows that little attention has ever been given to the abundant bryozoan assemblage which is conspicuously present within the group. The purpose of this report is to partially eradicate the deficiency by describing the specimens of fenestrate and pinnate forms which make up the bulk of Chouteau bryozoans.

A few workers have mentioned the presence of bryozoans in the Chouteau group, but no systematic study concerning them has yet been published. Moore (1928, p. 97) lists nine genera of Bryozoa as being present in the "Chouteau limestone (restricted)." They are as follows: "*Fistulipora* sp., *Batostomella* sp., *Lioclema* sp., *Fenestella* sp., *Pinnatopora* sp., *Ptilopora* sp., *Rhombopora* sp., *Streblotrypa* sp., and *Cystodictya* sp." In his faunal lists of the Sedalia limestone, Moore (1928, p. 155) records six genera and one species of *Fenestella*. They are as follows: "*Lioclema* sp., *Fenestella* sp., *Fenestella rudis* Ulrich, *Pinnatopora* sp., *Rhombopora* sp., *Ptilopora* sp., *Cystodictya* sp." The genera *Pinnatopora*, *Ptilopora* and *Cystodictya* are now considered as junior synonyms of *Penniretepora*, *Ptylopora*, and *Sulcoretepora* respectively (Bassler, 1953, p. 128 and 142).

The author's collection, which is in the Paleontological Museum of the University of Kansas, contains a bryozoan assemblage essentially similar to Moore's except for the questionable presence of *Penniretopora*. During the course of the work, several fragments of *Ptylopora* with the lateral branches broken off close to the main stem were observed. Such fragments are easily mistaken for specimens of *Penniretopora*. Inasmuch as specimens of *Penniretopora* were not found in the group, it does not mean that they may not be identified in the future.

The only other references to bryozoans in the Chouteau group are made by E. B. Branson in his work on the lower Mississippian of Missouri (1938, pt. 2, p. 185) and in his paper on the geology of Missouri (1944, p. 215). In both papers, there is a notation that *Evactinopora sexradiata* Meek & Worthen, 1868, is present in the Chouteau formation. The probable reason for this is that Branson considered nearly all the pre-Burlington post-Bushberg strata of Missouri as a part of the Chouteau formation. No representative of this distinctive genus was found by the author in the Chouteau group.

The family Fenestellidae is represented in the Chouteau group by eight species of *Fenestella*, four of which are new, and by two species of *Ptiloporella*, one of which is new. Several small fragments of *Polypora* were observed, but these were not sufficiently preserved to be identified specifically. The family Acanthocladiidae is represented by one specimen of *Ptylopora*.

All of the fenestrates found within the Chouteau group are considered by the author to be Kinderhookian in age because they show close affinities to both older Devonian and younger Mississippian forms, with the relationships to the latter being predominant. *Fenestella regalis* Ulrich and *F. rudis*

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Ulrich are present in rocks of Osagean and Meramecian age in Missouri, Illinois, Iowa, and Kentucky with the former also being present in the Cuyahoga formation in Ohio. *F. serratula* Ulrich, is common in the Chouteau group, and extends to the Chesterian.

The new species, *F. alternata*, *F. aequalis*, and *F. rotundata*, are related to forms described by Ulrich from the Keokuk of Iowa. *F. oblongata* which is also a new species is very much like *F. albida* Hall from the Waverly group in Ohio and is similar to another form described by Ulrich from the Burlington limestone of Iowa and Illinois. *F. parallela* Hall is a Devonian species which is also found in New York, Ohio, and Alabama. *Ptiloporella inaequalis* Hall & Simpson is reported from the Middle Devonian of Canada. The new species *Ptiloporella varia* appears to be a Devonian form in a penultimate stage of development. A related form, *Fenestella albida* var. *richfieldensis* Ulrich, which also retains vestiges of the ptiloporellid stock, occurs in the Waverly group in Ohio.

There has been such a variance of opinion concerning definition of the Chouteau group in years past that it is considered outside the scope of this paper to review the controversy at length. However, since most of the author's collection was made in the general area of Moore's type sections of the Chouteau limestone (restricted) and the Sedalia limestone, an attempt was made during the course of the field work in 1950 to determine the common contact of these two formations. The attempt was not successful because it was difficult to detect the presence of a contact anywhere in the rock succession that extends from the top of the Bushberg sandstone to the base of the Osagean formations within the area studied. The bryozoan assemblage also does not show any marked break which might indicate a discontinuity of the organic record. It is, therefore, assumed that if any contact does exist between the Chouteau limestone (restricted) and the Sedalia limestone as defined by Moore, it is of such transitional character that for all practical field purposes, such as mapping, it can be disregarded and that the rock succession can be considered as a single lithologic unit.

Other independent studies of this unit in the west-central and southwestern part of the state have also arrived at essentially similar conclusions. In 1950, Kaiser published a paper in which he recognizes the Chouteau limestone (restricted) and Sedalia dolomite as valid formations and distinct lithologic units, but he states (1950, p. 2151) that "in much of the area studied—the Sedalia dolomite lies conformably on the Chouteau limestone, and no evidence of a stratigraphic break between the two formations was found." He also classifies the Sedalia dolomite as Kinderhookian in age because, among other reasons given by him, he states (1950, p. 2151) that "most of the species that occur in the Sedalia dolomite are Kinderhookian forms very closely related to species found in the Chouteau limestone and the Chouteau and Sedalia formations represent a period of continuous deposition." Moore (1928, p. 150) considered the Sedalia formation to be Osagean in age. In 1951, Beveridge (p. 39) stated that in the Weaubleau Creek area "there is no local evidence of unconformity either above or below the Sedalia. The Chouteau is transitional, and—the fauna of the Chouteau and Sedalia appear similar and to represent facies change rather than any time interval between the two formations." In 1952, Clark & Beveridge published a preliminary report in which they proposed that the name Compton be substituted for Moore's Chouteau (restricted), that the Compton, Sedalia, and Northview formations be considered as parts of the Chouteau group, and that the top of the Kinderhookian series be drawn at the top of the Northview formation and, therefore, at the top of the Chouteau group (Clark & Beveridge, 1952, p. 71). One of the reasons they give for their proposal is that "to the north and east from central Pettis County, the Compton-Sedalia contact becomes obscure as these two formations interfinger and lose their lithologic contrasts which justify formational rank to the south. Also, the whole of the uppermost Northview formation passes laterally into the uppermost Sedalia or upper Chouteau in central Missouri. Therefore, in central and eastern Missouri, the three formations of western Missouri are generally indistinguishable and the Chouteau group (undifferentiated) is the most refined practical

mapping unit" (Clark & Beveridge, 1952, p. 74). In 1955, Bowsher, in a study of lower Mississippian camerate crinoids, stated (p. 5) that in southwestern Missouri he recognizes "the same sequence of lower Mississippian rocks as in the Weaubleau Creek area. The Chouteau seems here to grade upward into the Sedalia, which in turn grades laterally and vertically into the Northview shale." Because of the above considerations and the author's own conclusions, it is considered expedient for the purpose of this work to follow Clark & Beveridge in their definition and use of the term Chouteau group (undifferentiated).

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COLLECTING LOCALITIES

1. Quarry, 0.5 mile south of Dresden, Pettis County, Missouri. Section 28, T. 46 N., R. 22 W.
2. Quarry, 1.2 miles west of junction of West Main Street, Sedalia, Pettis County, Missouri, and U. S. Highway 50. Section 35, T. 46 N., R. 22 W.
3. Chouteau Springs, Cooper County, Missouri. Section 16, T. 48 N., R. 18 W.
4. Sweeney Quarry, 2.5 miles northeast of Clifton City, Cooper County, Missouri. Section 4, T. 46 N., R. 19 W.
5. Rocky Fork Creek, 3 miles northwest of Browns Station, Boone County, Missouri. Sections 28, 29, 32, 33, T. 50 N., R. 12 W.
6. Road cut, 0.75 mile southeast of Wilton, Boone County, Missouri. Section 26, T. 46 N., R. 13 W.
7. Railroad cut, 1 mile southeast of Wilton, Boone County, Missouri. Section 35, T. 46 N., R. 13 W.

SYSTEMATIC DESCRIPTIONS

Family FENESTELLIDAE King, 1850
Genus FENESTELLA Lonsdale, 1839
FENESTELLA ALTERNATA Koenig, n. sp.

Pl. 21, fig. 1; Text-figs. 1a,1b; Table 1

Zoarium a flexuous, fenestrate, somewhat palmate expansion. The largest specimen collected measures 25 mm. in length and 15 mm. in width. Branches on both sides of the median axis of the frond fan out in smooth curves and bifurcate at intervals of 2.5 mm. to 5.0 mm. The bifurcations are more frequent in the distal portions of the frond.

Branches moderately robust. Average branch width below a bifurcation 0.33 mm.; above, 0.25 mm. Total variability of branch width below a bifurcation 0.26 mm. to 0.39 mm.; above, 0.20 mm. to 0.33 mm. Ratio of branch width to fenestrule width about 1 to 1. Total variability of branches in 10 mm., 13 to 21. Obverse of branches gently convex, finely striated to smooth; no apparent keel development. Reverse of branches strongly convex to broadly arched, bearing medially, irregularly spaced, strong conical nodes of varying heights. Crowded nodes give reverse of branch a sharp angular appearance.

Dissepiments relatively strong. Width, approximately one-half that of branches. Average width 0.15 mm. Variability of width normally ranges from 0.11 mm. to 0.21 mm. Infrequently, dissepiments situated at positions equidistant from the base of the frond thicken to widths of 0.26 mm. to 0.30 mm. and thus form a prominent arc of thickened dissepiments across the back of the frond. Dissepiments on both sides of the frond are smooth, very finely striated when weathered, flush with the surface level of branches on the obverse and slightly depressed on the reverse.

Fenestrules quadrate to elongate-quadrate. Length very variable, ranging from 0.59 mm. to 0.90 mm.; average 0.74 mm. Width relatively constant at an average of 0.29 mm. Total variability of fenestrules in 10 mm., 9 to 16.

Zooecial apertures circular. Average diameter, 0.12 mm. They are alternately arranged and spaced one to two diameters apart longitudinally. A portion of the

TABLE 1—VARIABILITY OF MESHWORK OF *Fenestella alternata* KOENIG, N. SP.*

Locality No.	Specimen No.	Branches in 10 mm.	Fenestrules in 10 mm.	Apertures in 5 mm.	Nodes in 5 mm.
1	3-2	18–20	12–16		
3	3-19	20–21	14–16	18–19	18–19
	24-1	15–18	9–13		
4	13-1	15–17	12–14		
	16-1	15–16	13–15		
	18-2	17–21	10–12		
	39-6	16–17	12–13	18	18
5	2-3-1	17	13–15		
	3-12B-5	13	11–12		
	5 & 6-1′-8	17–19	12–15		
	8-3-47	16–19	13–15		
	8-4-23	16–18	12–15	17–19	17–19
6	10-1	14–18	10–15		
7	4-1	17–20	14–15		
Total variability		13–21	9–16	17–19	17–19

* Note: Specimen number: For localities 1 to 4, 6, and 7, the first part of the specimen number refers to a slab of rock from a given locality. The second part refers to a given specimen on the slab. For locality 5, the first part designates a collecting horizon, numbered 1 to 8 upward from the base of the Chouteau group. The second and third parts refer respectively to rock slab and specimen.

peristome on the inner part of the anterior margin of the aperture develops a small pointed process, and this feature gives the species its characteristic, alternate, nodose appearance. Total variability of apertures in 5 mm., 17 to 19.

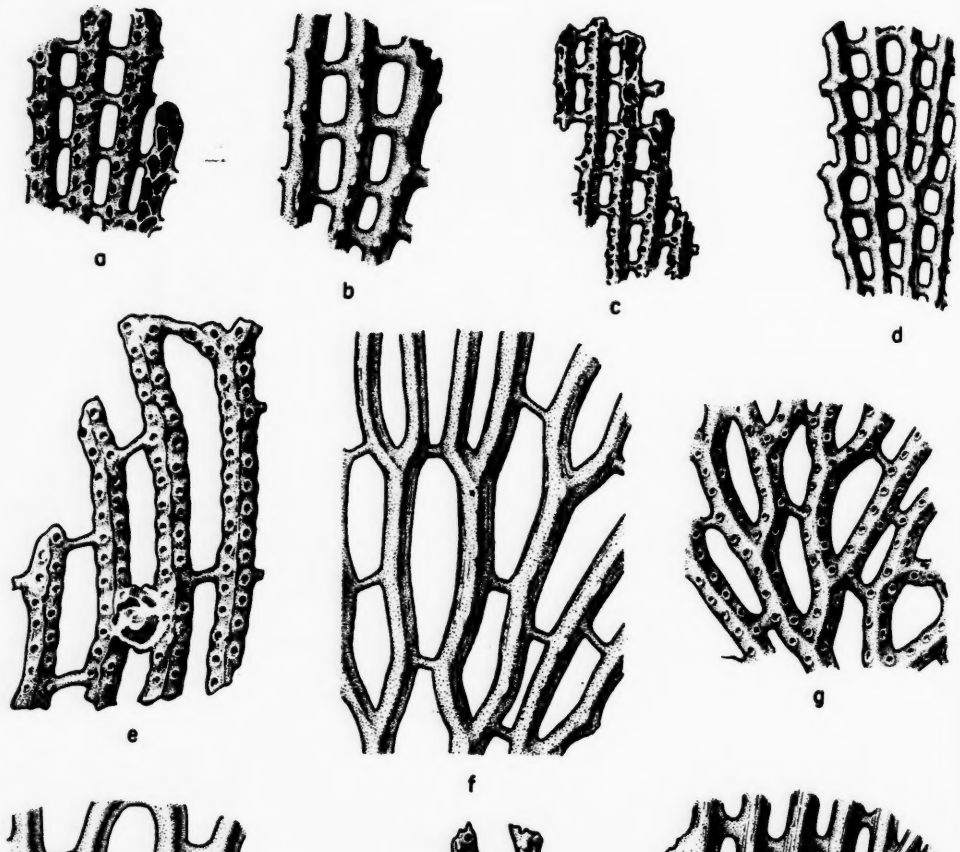
Discussion.—Except for its slightly thinner branches, its lack of a median keel, and its possession of small pointed processes on the anterior margins of the zooecial apertures, *F. alternata* is very similar to *F. limitaris* Ulrich from the Keokuk group at Bentonsport and Keokuk, Iowa. *F. limitaris* possesses a very weak to obsolete, sinuous median keel, alternating rows of zooecial apertures surrounded by prominent peristomes and flexuous branches which have a normal width of 0.35 to 0.40 mm. According to Ulrich (1890, p. 536–538), *F. limitaris* is also related to *F. rudis* Ulrich, which is a persistent species in the Chouteau, Keokuk, and Warsaw formations, and to *F. burlingtonensis* Ulrich of the Burlington limestone.

Occurrence.—*F. alternata* occurs throughout the Chouteau group and was found to be present at all collecting localities except one, locality 2, in Pettis County. Present at localities 1, 3 to 7.

FENESTELLA AEQUALIS Koenig, n. sp.
Pl. 21, fig. 2; pl. 22, fig. 1; Text-figs. 1c, 1d; Tables 2,3

Zoarium a fenestrate expansion of semiridged branches. The largest specimen collected measures 33 mm. in length and 27 mm. in width. Branches occupying the medial and distal portions of the frond are straight, subparallel, and bifurcate infrequently. Branches occupying the proximal portion of the frond are crowded and flexuous. They bifurcate frequently at intervals of 1.3 mm. to 3.5 mm., and their rate of expansion is greater near the base of the frond.

Branches moderately robust. Average width below a bifurcation 0.31 mm.; above, 0.22 mm. Total variability of branch width below a bifurcation 0.26 mm. to 0.35 mm.; above, 0.20 mm. to 0.24 mm. Ratio of branch width to fenestrule width about 1 to 1. Total variability of branches in 10 mm., 18 to 24. Obverse of branches angular, very finely pustulose, bearing small closely spaced conical nodes at the apex. Total variability of nodes in 5 mm., 25 to 30. Reverse of branches, sharply angular, finely pustulose with a prominent node developed oppo-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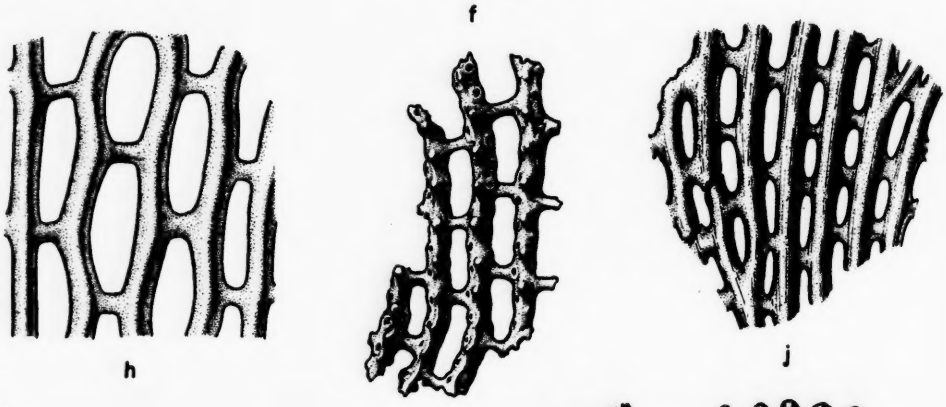
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TABLE 2—VARIABILITY OF MESHWORK OF *Fenestella aequalis* KOENIG, N. SP.

Locality No.	Specimen No.	Branches in 10 mm.	Fenestrules in 10 mm.	Apertures in 5 mm.	Nodes in 5 mm.
2	4-1	20–21	18–22		
4	52-12	19–21	18–24		
	53-8	23	17–20		
	19-1	19–23	19–21		
	25-2	20–21	17–20	22–23	26–29
5	2-1-1	20–21	18–19		
	5-5-1	21–24	16–22		
	5-1-1	21	18	23	25–29
	8-1-26	18–21	21–23	23–24	26–29
	8-12-1	21–23	21–22	21–23	26–30
Total variability		18–24	16–24	21–24	25–30

site the end of each dissepiment. Finely striated when weathered.

Dissepiments moderately strong. Width approximately one-half to two-thirds that of the branches in the proximal portion of frond and one-half to less than one-half in the medial and distal portions. Width averaging 0.14 mm., but varying from 0.10 mm. to 0.20 mm. The development of an abnormally thickened dissepimental arc across the reverse of the frond is similar to that in *F. alternata*. Dissepiments on obverse strongly convex, smooth, slightly depressed below the level of the branches; on reverse, sharply angular, finely pustulose, flush to elevated above surface level of branches. Finely striated when weathered.

Fenestrules suboval in the proximal portion of the frond and quadrate to subquadrate in the medial and distal portions. Length of fenestrules moderately variable, averaging 0.55 mm. long. Width relatively constant at an average of 0.26 mm. Total variability of fenestrules in 10 mm., 16 to 24.

Zooecial apertures small, circular. Average diameter, 0.08 mm. Alternately arranged and spaced one to one and one-half diameters apart longitudinally. Total variability of apertures in 5 mm., 21 to 24. Peristome obsolete.

Discussion.—In the overall shape and arrangement of related frond constituents, *F. aequalis* very closely resembles *F. multispinosa* Ulrich from the Keokuk group of Iowa and Kentucky. However, *F. aequalis* tends to have a slightly finer mesh work than *F. multispinosa*, and other variations tend to differentiate the two species. In *F. multispinosa*, the apertures are "seemingly sit-

EXPLANATION OF TEXT-FIG. *1*
All figures ×10

FIG. *1a,1b—Fenestella alternata* Koenig, n. sp. *1a*, obverse view of paratype, K. U. 10169-B-7. *1b*, reverse view of paratype, K. U. 10169-A.
1c,1d—Fenestella aequalis Koenig, n. sp. *1c*, obverse view of paratype, K. U. 10168-B-8. *1d*, reverse view of holotype, K. U. 10168-B-7.
1e,1f—Fenestella oblongata Koenig, n. sp. *1e*, obverse view of paratype, K. U. 10169-B-6. *1f*, reverse view of holotype, K. U. 10169-B-5.
1g,1h—Fenestella regalis Ulrich. *1g*, obverse view of specimen, K. U. 10168-G. *1h*, reverse view of specimen, K. U. 10169-E.
1i,1j—Fenestella rudis Ulrich. *1i*, obverse view of specimen, K. U. 10168-F. *1j*, reverse view of specimen, K. U. 10167-B.
1k,1l—Fenestella rotundata Koenig, n. sp. *1k*, obverse view of holotype, K. U. 10170-B-10. *1l*, reverse view of paratype, K. U. 10169-B-9.
1m,1n—Fenestella serratula Ulrich. *1m*, obverse view of specimen, K. U. 10168-D. *1n*, reverse view of specimen, K. U. 10168-E.

TABLE 3—COMPARATIVE VARIABILITY OF MESHWORKS OF *Fenestella serrata*, *F. aequalis*, AND *F. multispinosa*

Species	Branches in 10 mm.	Fenestrules in 10 mm.	Apertures in 5 mm.	Nodes in 5 mm.
F. serrata Hall, 1883 Hamilton gp. (M. Dev.)	20–24	16–18	22+	22+
F. aequalis Koenig, n. sp. Chouteau gp. (Kinderhookian)	18–24	16–24	21–24	25–30
F. multispinosa Ulrich, 1890 Keokuk gp. (Osagean)	20–21	13–15	21	21
F. multispinosa var. *chesterensis* Condra & Elias, 1944 (Chesterian)	15–20	13–15	20–24	abt. 18

uated in a groove at the base of the keel, with the outer margin prominent, sometimes appearing almost spine-like" (Ulrich, 1890, p. 541), whereas, in *F. aequalis* the peristomes are obsolete, and the apertures are flush with the sloping obverse surfaces of the branches. In *F. multispinosa*, the reverse of the branches is convex and "covered with granose longitudinal striae" (Ulrich, 1890, p. 541), whereas in *F. aequalis* the branches is strongly angular and covered with a more or less uniform granose or a finely pustulose surface.

F. serrata Hall, from the Hamilton group near the Falls of the Ohio resembles *F. aequalis* in overall size and shape, but in the species *F. serrata* the reverse of the branches are convex to subangular with irregularly arranged, prominent nodes, and the obverse portion of the dissepiments is more acutely angular.

From these comparisons, *F. aequalis* might be considered as a transitional form between *F. serrata* of the Middle Devonian and *F. multispinosa* of the Lower Mississippian (Osagean). The younger species possesses a slightly coarser mesh work than *F. aequalis*, and it is interesting to note that occurrences of *F. multispinosa* in still younger formations have a tendency to be slightly coarser still as shown in Table 3.

A slight similarity exists between *F. aequalis* and *F. exigua* Ulrich in that both species possess a prominent node opposite the end of each dissepiment on the reverse side of the branches. When the ends of two adjacent dissepiments oppose each other the corresponding nodes coalesce and form a pronounced ridge on the branch.

Occurrence.—*F. aequalis* is present throughout the Chouteau group at localities 2, 4, and 5.

FENESTELLA OBLONGATA Koenig, n. sp.
Pl. 21, fig. 4; Text-figs. 1e,1f; Tables 4, 5

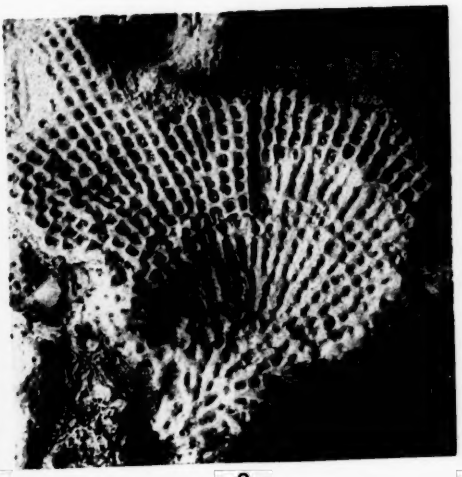
Zoarium a lax fenestrate expansion of irregularly arranged, slender branches and dissepiments. The branches are sinuous to straight, variably spaced, and they bifurcate at intervals of 4.0 to 5.0 mm.

Branches relatively thin. Average branch width below a bifurcation 0.39 mm.; above, 0.31 mm. Ratio of branch width to fenestrule width about 1 to 2. Total variability of

EXPLANATION OF PLATE 21

FIG. *1*—*Fenestella alternata* Koenig, n. sp. Reverse view of holotype, K. U. 10170-B-1. ×2.67.
2—*Fenestella aequalis* Koenig, n. sp. Reverse view of holotype, K. U. 10168-B-7. ×4.
3—*Fenestella parallela* Hall. Reverse view of specimen, K. U. 10169-C. ×2.
4—*Fenestella oblongata* Koenig, n. sp. Reverse view of holotype, K. U. 10169-B-5. ×2.67.
5—*Fenestella serratula* Ulrich. Obverse view of specimen, K. U. 10168-D. ×4.
6—*Ptiloporella inaequalis* (Hall & Simpson). Reverse view of specimen. K. U. 10169-K. ×4.
7—*Fenestella rudis* Ulrich. Reverse view of specimen, K. U. 10167-B. ×2.67.

1



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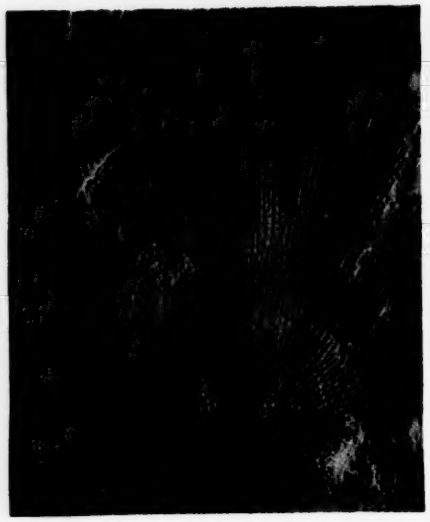

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TABLE 4—VARIABILITY OF MESHWORK OF *Fenestella oblongata* KOENIG, N. SP.

Locality No.	Specimen No.	Branches in 10 mm.	Fenestrules in 10 mm.	Apertures in 5 mm.	Nodes in 5 mm.
3	3-15	10–11	5–6	14–15	6–7
4	52-6	12–13	7	17	6–7
	52-9	9–10	4–5	15	
5	2-24-1			17	4
	2-20-2	9		15–16	5
7	7-1	13–15	6–7	18–19	7
Total variability		9–15	4–7	14–19	4–7

TABLE 5—COMPARATIVE VARIABILITY OF MESHWORKS OF *Fenestella filistriata*, *F. oblongata*, AND *F. albida*

Species	Branches in 10 mm.	Fenestrules in 10 mm.	Apertures in 5 mm.	Nodes in 5 mm.
F. filistriata Ulrich, 1890 Burlington ls. Iowa & Illinois	13	6	13–14	none
F. oblongata Koenig, n. sp. Chouteau gp. Missouri	9–15 (avg. 12)	4–7 (avg. 6)	14–19 (avg. 16)	4–7 (avg. 6)
F. albida Hall, 1887 Waverly gp. Ohio	15–16	6	16–17	4

branches in 10 mm., 9 to 15. Obverse of branches gently convex, very finely striated. Small widely spaced nodes are present on a thin, almost obsolete medial keel. Reverse of branches, subangular, very finely granulose, bearing infrequent conical nodes.

Dissepiments slender. Width approximately one-third that of the branches. Average width, 0.11 mm. Dissepiments round, smooth, and slightly depressed below the surface level of the branches on both sides of the frond.

Fenestrules generally elongate-elliptical to elongate-quadrate but frequently irregular in shape. Length extremely variable, ranging from 0.65 mm. to 2.50 mm.; average 1.67 mm. Width also exceedingly variable, ranging from 0.20 mm. to 0.78 mm.; average 0.48 mm. Total variability of fenestrules in 10 mm., 4 to 7.

Zooecial apertures circular. Average diameter 0.11 mm. They are alternately arranged and spaced one to two diameters apart longitudinally. Peristomes prominent; beaded in appearance. Total variability of apertures in 5 mm., 14 to 19.

EXPLANATION OF PLATE 22

FIG. *1*—*Fenestella aequalis* Koenig, n. sp. Reverse view of paratype, K. U. 10169-D. ×2.
2—*Fenestella regalis* Ulrich. Reverse view of specimen, K. U. 10169-E. ×1.
3—*Ptiloporella varia* Koenig, n. sp. Reverse view of medial and distal part of frond of paratype, K. U. 10168-B-11. ×2.
4—*Ptiloporella varia* Koenig, n. sp. Reverse view of proximal part of frond of holotype. K. U. 10169-H. ×2.67.
5—*Ptylopora* sp. Reverse view of specimen, K. U. 10168-A. ×4.
6—*Fenestella regalis* Ulrich. Reverse view of proximal part of frond of specimen, K. U. 10169-F. ×1.

Nodes on both sides of frond, low, conical, widely spaced. Nodes on reverse frequently present immediately below a bifurcation. Total variability of nodes on observe in 5 mm., 4 to 7.

Discussion.—This species bears a close resemblance to *F. albida* Hall from the Waverly group of Ohio, and is also related to *F. filistriata* Ulrich from the Burlington group of Iowa and Illinois. It differs from the former by having a more open, irregular meshwork with fewer branches per centimeter and a less pronounced parallelism of the branches. It also differs in having more nodes in 5 mm. on the obverse median keel and an irregular nodal development on the reverse. The presence of nodes distinguishes it from *F. filistriata* Ulrich, which is described as being free of such features, and it has more closely spaced apertures than *F. filistriata.*

Occurrence.—*F. oblongata* is present throughout the Chouteau group at localities 3, 4, 5, and 7.

FENESTELLA REGALIS Ulrich, 1890

Pl. 22, figs. 2,6; Text-figs. 1g,1h; Table 6

1888 *Fenestella regalis* Ulrich, Bull. Denison Univ., v. 4, pt. 1, p. 70–71.

1890 *Fenestella regalis* Ulrich, Geol. Surv. Ill., v. 8, p. 538–539, pl. 50, figs. 1,1a, pl. 54, fig. 5.

Zoarium a large, strong, flabellate, fenestrate expansion. The largest specimen collected measures approximately 80 mm. in length and width. Branches subsinuous and symmetrically arranged above a strong stem-like base 1.2 mm. in diameter which diminishes in width distally to 0.58 mm. in a distance of 7.0 mm. to form the medial branch of the frond. Branches bifurcate at intervals of 4.0 to 6.0 mm.

Branches exceptionally strong. Average branch width below a bifurcation 0.50 mm.; above, 0.36 mm. Maximum branch width measured, 0.65 mm. Ratio of branch width to fenestrule width 1 to 1.5. Total variability of branches in 10 mm., 9 to 18. Obverse of branches, subangular, strongly striated; no apparent keel development and small nodes infrequently present. Generally, in the proximal part of the frond the nodes are spaced approximately 0.5 mm. apart. Total variability of nodes in 5 mm., 11 to 13. Reverse of branches strongly angular and striated.

Dissepiments very strong. Width normally two-thirds that of the branches, but in some instances a one to one ratio prevails. Average width, 0.30 mm. An abnormally thickened dissepimental arc is developed across the reverse of the frond as in *F. aequalis* and *F. alternata* except that in *F. regalis* adjacent sets of dissepiments are involved, and the included fenestrules are noticeably shortened. Dissepiments on both sides of the frond are gently convex, smooth, finely striated when weathered, and slightly depressed to flush with the surface level of the branches.

Fenestrules quadrate to elongate to elliptical. Length variable, ranging from 1.0 mm. to 2.0 mm. Width relatively constant at an average of 0.65 mm., varying from 0.52 mm. to 0.78 mm. Total variability of fenestrules in 10 mm., 5 to 10.

Zooecial apertures circular. Average diameter 0.12 mm. They are alternately arranged and spaced one and one-half diameters apart longitudinally. Peristomes prominent, beaded in appearance. Total variability of apertures in 5 mm., 16 to 19.

Discussion.—The exceptionally large size of the branches and fenestrules of this spe-

TABLE 6—VARIABILITY OF MESHWORK OF *Fenestella regalis* ULRICH, 1890

Locality No.	Specimen No.	Branches in 10 mm.	Fenestrules in 10 mm.	Apertures in 5 mm.	Nodes in 5 mm.
4	48-5	17–18	8	16–17	11–13
	14-3	11–13	8–10	17–18	
	6-1	10	5–6	18–19	
5	2-21-1	9–13	5–7		
	2-25-1	10–13	5–7		
Total variability		9–18	5–10	16–19	11–13

TABLE 7—VARIABILITY OF MESHWORK OF *Fenestella rotundata* KOENIG, N. SP.

Locality No.	Specimen No.	Branches in 10 mm.	Fenestrules in 10 mm.	Apertures in 5 mm.	Nodes in 5 mm.
5	12B-10	20–26	21–25		
6	1-1	18–20	19–21	18–19	18–19
Total variability		18–26	19–25	18–19	18–19

cies make it particularly distinctive. The characteristics of the specimens found in the Chouteau group accord very closely with Ulrich's original description and illustrations of the holotype from the Keokuk group at King's Mt. Tunnel, Kentucky, and with his notations of specimens from the Cuyahoga shale at Richfield and Lodi, Ohio. Ulrich (1890, p. 539), in his description of the type specimens, notes the presence of a strong rounded carina "bearing a row of small nodes about 0.8 mm. apart." This feature is not strongly developed in any of the Chouteau forms in as much as the keel or carina appears to be obsolete and the nodes infrequently and poorly developed. A few specimens possess scattered groups of low conical nodes that are generally spaced from 0.4 mm. to 0.5 mm. apart on a very weak to obsolete carina. This feature of the Chouteau forms does not seem to be of sufficient weight to warrant the designation of a new species.

The Chouteau specimens also exhibit close affinities to *F. noe* (Hall & Simpson) from the New Scotland limestone (Helderberg) of New York. The two forms possess comparable measurements, proportions, and surficial characteristics, but they differ in that *F. noe* exhibits more slender and less flexuous branches.

Occurrence.—*F. regalis* is present throughout the Chouteau group at localities 1 to 5.

FENESTELLA ROTUNDATA Koenig, n. sp.
Text-figs. 1k,1l; Table 7

Zoarium a strong, closely knit, fenestrate expansion. Only two small fragments of this species were observed, consequently, the form of a fully developed zoarium is conjectural. The straight, rigid branches in both specimens are closely spaced and parallel.

Branches broad and strong. The average branch width below a bifurcation is 0.69 mm.; above, 0.45 mm. The branch width increases rapidly above a bifurcation and soon attains a uniform width of 0.57 mm. Ratio of branch width to fenestrule width is 1.5 to 1. Total variability of branches in 10 mm., 18 to 26. Obverse of branches, broadly rounded and smooth. No mesial keel is developed, but nodes are prominent and slightly elongate at the base. Total variability of nodes in 5 mm., 18 to 19. Reverse of branches, broadly rounded and strongly striated.

Dissepiments are wider on obverse than on reverse. Average width, 0.17 mm. On the obverse, dissepiments are strongly striated and slightly depressed below the level of the branches. On the reverse, they are striated and strongly depressed.

Fenestrules quadrate to round. Average length and width, 0.43 mm. Total variability of fenestrules in 10 mm., 19 to 25.

Zooecial apertures small, circular. Average diameter 0.09 mm. They are spaced about one and one-half diameters apart longitudinally. Total variability of apertures in 5 mm., 18 to 19. Peristomes well developed. Their outer margins extended slightly into the fenestrules.

Discussion.—This species is comparable to *F. multispinosa* Ulrich and to *F. serratula* Ulrich. Its main distinction from the former species is in its smaller and shorter fenestrule and, therefore, in its possession of more fenestrules in 10 mm. *F. multispinosa* has from 14 to 15 fenestrules in that distance, and *F. rotundata* has 19 to 25. This same feature distinguishes it from *F. serratula* which possesses 14 to 18 fenestrules in 10 mm. *F. serratula* is also more delicate, and its branches are much thinner.

Occurrence.—*F. rotundata* is present in the Chouteau group at localities 5 and 6.

FENESTELLA RUDIS Ulrich, 1890
Pl. 21, fig. 7; Text-figs. 1i,1j; Table 8

1890 *Fenetella rudis* Ulrich, Geol. Surv. Ill., v. 8, p. 537, pl. 48, figs. 3–3d.
1894 *Fenestella rudis* Keys, Mo. Geol. Surv., v. 5, p. 23, pl. 34, fig. 5.
1906 *Fenestella rudis* Cumings, Ind. Dept. Geology and Nat. Resources, 30th Ann. Rept., p. 1277, pl. 27, figs. 3–3d.

Zoarium a large flabellate expansion. The branches are regularly spaced and subparallel. They expand slowly and bifurcate infrequently. They are straight and rigid except in the marginal portions of the frond where they bend slightly.

Branches moderately strong. Average width below a bifurcation 0.33 mm.; above, 0.26 mm. Ratio of branch width to fenestrule width about 1 to 1. Total variability of branches in 10 mm., 13 to 17. Obverse of branches, angular, finely striated longitudinally, bearing strong, conical nodes along the apex. Total variability of nodes in 5 mm., 14 to 15. Reverse broadly convex and finely striated.

Dissepiments relatively weak. Width approximately one-third to one-half that of the branches. Average width 0.12 mm. Dissepiments rounded, faintly striated, and slightly depressed below the level of the branches on both obverse and reverse.

Fenestrules on the obverse, quadrate to elongate-quadrate; on the reverse they appear elongate elliptical. Average length 1.04 mm.; average width 0.34 mm. Total variability of fenestrules in 10 mm., 6 to 10.

Zooecial apertures circular. Average diameter, 0.11 mm. They are spaced one and one-half to two diameters apart longitudinally. Peristomes, prominent, projecting slightly into the fenestrules. Total variability of apertures in 5 mm., 10 to 14.

Discussion.—Representatives of this species from the Chouteau group fit Ulrich's original description rather closely except for the number and spacing of the zooecial apertures. Ulrich (1890, p. 537) describes specimens of the species from the Keokuk and Warsaw formations as having 18 zooecial apertures in 5 mm. This number of apertures obviously does not represent the total variability for the species because Cumings (1906, p. 1277) describes specimens from the Salem limestone of Indiana that possess 22 zooecial apertures in 5 mm., and the specimens from the Chouteau group exhibit from 10 to 14 apertures in that distance. It is possible that this increase in the number of apertures represents an evolutionary development. Another interesting feature in the three reported occurrences is the nodal development on the reverse of the frond. Specimens from the Chouteau group do not show nodes on the reverse. Ulrich (1890, p. 537) states that specimens from the Keokuk and Warsaw formations are "often irregularly tubercalose" on the reverse of the branches, and "at other times" the branches are "only thickened at their junction with the dissepiments." Cumings (1906, p. 1277) describes specimens from the Salem limestone as having "a number of large low spines to the fenestrule, especially at the angles of the fenestrules" on the reverse of the branches.

Occurrence.—*Fenestella rudis* is found in the middle part of the Chouteau group at localities 3 and 4, and in the lower part of the group at locality 5.

TABLE 8—VARIABILITY OF MESHWORK OF *Fenestella rudis* ULRICH, 1890

Locality No.	Specimen No.	Branches in 10 mm.	Fenestrules in 10 mm.	Apertures in 5 mm.	Nodes in 5 mm.
3	3-25	13–20	8–9		
	27-2	13–17	9–10	14	
4	7-2	16–17	9–10	10–11	14–15
	9-1	14–17	8–9		
5	2-5	17	6–8		
	12-5	14–15	8–9		
Total variability		13–17	6–10	10–14	14–15

FENESTELLA SERRATULA Ulrich, 1890
Pl. 21, fig. 5; Text-figs. 1m,1n;
Tables 9,10

1890 *Fenestella serratula*, Ulrich, Geol. Surv. Ill., v. 8, p. 544, pl. 50, figs. 5–5c.
1894 *Fenestella serratula* Keys, Mo. Geol. Surv., v. 5, p. 23.
1906 *Fenestella serratula* Cumings, Ind. Dept. Geology and Nat. Resources, 30th Ann. Rept., p. 1280, pl. 30, figs. 2–2c,3,3a.
1944 *Fenestella serratula*, Condra & Elias, Geol. Soc. America Spec. Paper 53, p. 72–76, pl. 13, figs. 6–8; pl. 21, figs. 4,5; pl. 36, fig. 3.

Zoarium a flat, closely knit, flabellate expansion. The branches are straight, rigid, parallel, and expand gradually. In the medial and distal parts of the frond, the intervals between bifurcations are infrequent, but in the proximal portion, they divide at intervals of 1.8 mm., to 4.0 mm.

Branches narrow and weak. They have an almost uniform width of 0.25 mm. throughout their length. Ratio of branch width to fenestrule width about 2 to 1. Total variability of branches in 10 mm., 17 to 26. Obverse of branches flat with faintly striated interapertural surfaces sloping gently away from either side of a low, thin keel which bears rather small, slightly elongate nodes. The nodes are closely spaced at intervals of 0.16 mm. to 0.19 mm. Total variability of nodes in 5 mm., 27 to 30. Reverse moderately convex and granulo-striated.

Dissepiments weak. Width approximately one-third to one-half as wide as the branches. Average width 0.10 mm. Dissepiments slightly depressed below the level of the branches on both sides of the frond, round, faintly striated, and regularly arranged at right angles to the branches.

Fenestrules narrow, elongate-quadrate. Length fairly constant, ranging from 0.52 mm. to 0.64 mm. Width fairly uniform throughout the frond, ranging from 0.13 mm. to 0.19 mm. Total variability of fenestrules in 10 mm., 14 to 18.

Zooecial apertures small, circular. Average diameter 0.08 mm. They are spaced approximately one and one-third diameters apart longitudinally. Peristomes, prominent where well preserved. Total variability of apertures in 5 mm., 18 to 23.

Discussion.—This interesting species is a persistent form in Mississippian rocks and is easily recognized because of its close-knit, delicate frond. Although the specimens from the Chouteau group have a slightly coarser meshwork than other described specimens, it is judged that this distinction is not of sufficient importance to warrant the designation of a new species when all major

TABLE 9—COMPARATIVE VARIABILITY OF MESHWORKS OF *Fenestella serratula* AND *F. cumingsi*

Species & Reference	Formation & Location	Branches in 10 mm.	Fenestrules in 10 mm.	Apertures in 5 mm.	Nodes in 5 mm.
F. serratula Koenig, n. sp.	Chouteau gp., Mo.	17–26	14–18	18–23	27–30
F. serratula Ulrich, 1890, p. 545	Warsaw beds, Ill.	25–26	18–19	25–26	25–26
F. serratula Ulrich, 1890 p. 545	Chester gp., Ky.	(25–26)	17–18	24–25	(24–25)
F. serratula Condra & Elias, 1944, p. 73	Warsaw beds, Ill.	22–30	17–24	25–28	20–28
F. serratula Condra & Elias, 1944, p. 74	Chester sers., Ill.; Paradise fm., Ariz.	22–27 20–25	19–24 18–24	22–26 22–26	 15–25
F. serratula Cumings, 1906, p. 1280	Salem ls., Ind.	22–26	15–20	22	22
F. cumingsi Condra & Elias, 1944, p. 103	Chester sers., Ill.; Paradise fm., Ariz.	20–25 20–22	16–19 16–18	22–25 22–25	 25–26

TABLE 10—VARIABILITY OF MESHWORK OF *Fenestella serratula* ULRICH, 1890

Locality No.	Specimen No.	Branches in 10 mm.	Fenestrules in 10 mm.	Apertures in 5 mm.	Nodes in 5 mm.
2	2-1	19–23	14–15		
4	48-4	17–19	16–18	18–19	29
	5-2	21–25	14–18		
	14-1	26	14–16	22–23	27–30
5	10-1	21–24	14	19–22	27–29
	5-1	23–25	15–17		
Total variability		17–26	14–18	18–23	27–30

features are so similar to the ones described by Ulrich in his original definition of the species. Indeed, if the specimens of the Chouteau group were to be considered on the basis of their fenestrule count alone, they would be more comparable to *F. cumingsi* Condra & Elias, which is found in the Chester series of Illinois and in the Paradise formation of Arizona. *F. cumingsi* has a variability of 16 to 19 fenestrules in 10 mm., whereas the Chouteau specimens of *F. serratula* have 14 to 18 fenestrules in the same distance. The average Warsaw and Chester specimens of *F. serratula*, as described by Condra & Elias, have 17 to 24 fenestrules in 10 mm. Ulrich (1890, p. 545) considered the Chester forms which possess from "seventeen to eighteen fenestrules in 1 cm." to be larger than the forms reported by him from the Warsaw, Keokuk, and St. Louis limestones. Condra & Elias consider this larger form to be distinctive, and they accordingly designate it as a different species, although they state (1944, p. 104) that aside from the larger fenestrules "there seems to be no other differences between zoaria of *F. serratula* and *F. cumingsi*." Conversly, by omission, they seem to accept as valid the specimens described by Cumings as *F. serratula* from the Salem limestone of Indiana. Cumings (1906, p. 1280) states that his specimens possess from "15 to 20 fenestrules per centimeter." This number of fenestrules in 10 mm. is essentially the same as those specified by Condra & Elias (1944, p. 103) for *F. cumingsi*—16 to 19 fenestrules in 10 mm.

The author believes that because of the close similarity of the features of the specimens described as *F. serratula* and *F. cumingsi* that there is no need for specific distinction of the larger forms, and that the total variability of the number of fenestrules in 10 mm. for the species *F. serratula* ranges from 14 to 24. These relationships are shown in Table 9.

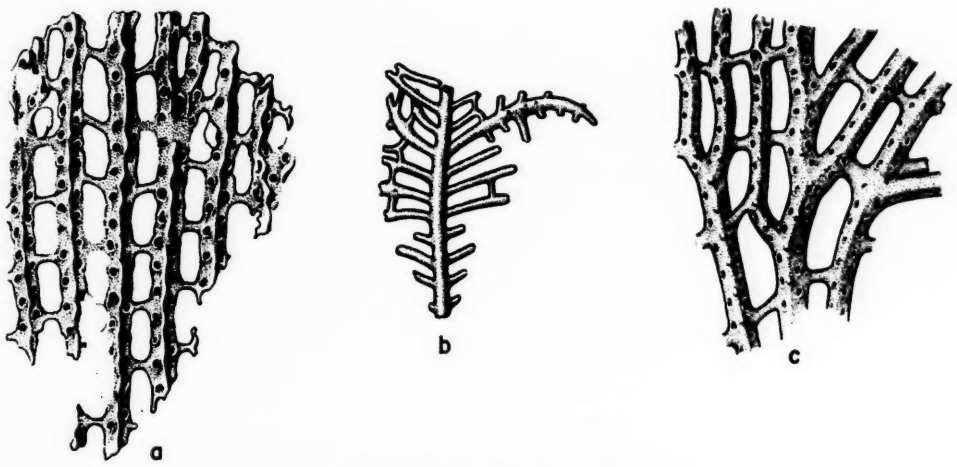
Occurrence.—*F. serratula* is present throughout the Chouteau group at localities 2, 4, and 5.

FENESTELLA PARALLELA Hall, 1885
Pl. 21, fig. 3; Text-fig. 2a; Table 11

1885 *Fenestella parallela* Hall, Rept. State Geologist (New York) for the year 1884, pl. 1, fig. 7.
1886 *Fenestella parallela*, Hall, Fifth Ann. Rept. State Geologist (New York) for the year 1885, pl. 44, figs. 8–18.
1887 *Fenestella parallela*, Hall & Simpson, Paleontology of New York, v. 6, p. 107, pl. 44, figs. 8–18.

Zoarium a flabellate expansion. The branches are straight and subparallel. They expand gradually and bifurcate at infrequent intervals.

Branches moderately robust. Average branch width below a bifurcation 0.35 mm.; above, 0.26 mm. Ratio of branch width to fenestrule width about 1 to 1. Total variability of branches in 10 mm., 15 to 21. The obverse side of the branches varies in degree of angularity. Some specimens possess rather flat interapertural surfaces which slope away from the mesial keel at a low angle, whereas, the same surfaces on other specimens have a much more pronounced inclination. The keel is not prominent between the strong, thin, elongate nodes which it supports. The keel and nodes appear as one thin structure which is decidedly serrate when viewed in profile. The nodes are so spaced that there is from two and one-half



EXPLANATION OF TEXT-FIG. 2

FIG. 2a—*Fenestella parallela* Hall. Obverse view of specimen, K. U. 10168-B-3. ×10.
2b—*Ptylopora* sp. Reverse view of specimen, K. U. 10168-A. ×4.
2c—*Ptiloporella varia* Koenig, n. sp. Obverse view of paratype, K. U. 10169-J. ×10.

to three nodes in the space of 1 mm. The total variability of nodes in 5 mm., is 12 to 18. The reverse of the branches is round and smooth but becomes very coarsely striated when weathered.

Dissepiments moderately strong. Width approximately one-half as wide as the branches. Dissepiments round, faintly striated, and slightly depressed on the obverse, but strongly depressed on the reverse.

Fenestrules quadrate. The ratio of fenestrule length to width is about 2 to 1. The average length is approximately 0.68 mm., and the width is about 0.25 mm. Total variability of fenestrules in 10 mm. is 12 to 19.

Zooecial apertures circular. Average diameter 0.12 mm. They are alternately arranged and spaced a little more than one diameter apart longitudinally. The peristomes are undeveloped. Total variability of apertures in 5 mm. is 16 to 18.

Discussion.—There is no question as to the identification of this species because the specimens examined compare very closely with the descriptions and illustrations prepared by Hall & Simpson for specimens from the Middle Devonian of New York, Ohio, and Alabama. From Hall & Simpson's data the following variability counts can be derived for the four basic elements of the frond: 17 to 20 branches in 10 mm., 12 to 13 fenestrules in 10 mm., 16 zooecial apertures in 5 mm., and 20 obverse nodes in 5 mm. The corresponding counts for specimens from the Chouteau group are as follows: 15 to 21 branches in 10 mm., 12 to 19 fenestrules in

TABLE 11—VARIABILITY OF MESHWORK OF *Fenestella parallela* HALL, 1885

Locality No.	Specimen No.	Branches in 10 mm.	Fenestrules in 10 mm.	Apertures in 5 mm.	Nodes in 5 mm.
4	39-5′	15–17	13–14	16–17	12–13
	14-4	17–20	12–13	17–18	13–15
5	9-1	16–20	15–17	16	14–15
	20-1	17–18	15–17	16–18	17–19
7	19-21	15–19			
Total variability		15–21	12–19	16–18	12–18

10 mm., 16 to 18 zooecial apertures in 5 mm., and 12 to 18 obverse nodes in 5 mm. Branch and fenestrule measurements also correspond closely, and the overall shape and arrangement of the frond meshwork is similar.

This species is closely related to *Fenestella alternata* but is distinguished from that species by its thin, serrate keel, shorter fenestrule length, and more rigid, parallel branches.

Occurrence.—*Fenestella parallela* is found in the lower and middle part of the Chouteau group at locality 4, and in the lower part of the group at localities 5 and 7.

Genus PTILOPORELLA Hall, 1885
PTILOPORELLA INAEQUALIS (Hall & Simpson), 1887
Pl. 21, fig. 6; Table 12

1887 *Fenestella* (*Ptiloporella*) *inaequalis* Hall & Simpson, Paleontology of New York, v. 6, p. 171.

1897 *Ptiloporella inaequalis* Simpson, Fourteenth Ann. Rept. State Geologist (New York) for the year 1894, pl. 6, figs. 1,2.

Zoarium a flabellate expansion consisting of straight, subparallel primary and secondary branches. The primary branches radiate outward from a common center like ribs of an open fan.

Primary branches strong, round, and finely granulose; striated when weathered. They increase in width distally from 0.33 mm. to 0.54 mm. The secondary branches are similar in appearance to the primaries but are less strong. They increase in width distally from 0.20 mm. to 0.26 mm. The branches are regularly spaced. Ratio of branch width to fenestrule width is 1 to 1.25. Total variability of secondary branches in 10 mm., 19 to 27.

Dissepiments weak, round, and finely granulose; faintly striated when weathered. Width generally one-half as wide as the secondary branches. Average width approximately 0.12 mm. Dissepiments flush with the level of the secondary branches and slightly depressed below the level of the primaries.

Fenestrules subquadrate to quadrate. Their lengths are variable and range from 0.39 mm. to 0.78 mm. However, the majority of fenestrules are approximately 0.58 mm. in length. Their widths range from 0.24 mm. to 0.33 mm. Total variability of fenestrules in 10 mm., 12 to 16.

Discussion.—Only the reverse side of three specimens of this species was observed; thus, the size, number, and arrangement of zooecial apertures and other obverse features are unknown. However, the regular pattern and arrangement of the branches and fenestrules of the three specimens observed make them quite distinct from fragments of *Ptiloporella varia*. Also, except for the slightly greater average length of the fenestrules, the specimens from the Chouteau group agree very closely with the original descriptions and figures presented by Hall and Simpson for specimens of the species from the Middle Devonian of Canada.

Occurrence.—*Ptiloporella inequalis* occurs in the lower part of the group at locality 3, and in the lower and upper part of the group at locality 5.

PTILOPORELLA VARIA Koenig, n. sp.
Pl. 22, figs. 3,4; Text-fig. 2c; Table 13

Zoarium a broad, flabellate expansion. The branches in the vicinity of the medial axis of the frond are relatively straight while the branches on either side fan out in broad sweeping arcs. There is no definite arrange-

TABLE 12—VARIABILITY OF MESHWORK OF *Ptiloporella inaequalis* (HALL & SIMPSON), 1887

Locality No.	Specimen No.	Branches in 10 mm.	Fenestrules in 10 mm.	Apertures in 5 mm.	Nodes in 5 mm.
3	22-6	19–21	15–16		
5	25-2	19–20	12–13		
	10-5	21–27	12–15		
Total variability		19–27	12–16		

TABLE 13—VARIABILITY OF MESHWORK OF *Ptiloporella varia* KOENIG, N. SP.

Locality No.	Specimen No.	Branches in 10 mm.	Fenestrules in 10 mm.	Apertures in 5 mm.	Nodes in 5 mm.
2	6-1	12	8–10		
4	23-1	14–17	7–8		
	29-1		7–8	16–17	14–15
5	8-14	14–19	8–9	19	14
	5-5	17	9–10		
	1-1	17	7–8	17–18	9–10
Total variability		12–17	7–10	16–19	9–15

ment of the primary and secondary branches in the distal part of the frond. Here they are distinguished with difficulty because the secondary branches expand to approximately the same width as the primary branches within a short distance and in turn give rise to rapidly enlarging tertiary branches which quickly assume the size of secondaries. The distinction of primaries and secondaries is more apparent in the proximal and medial parts of the frond. In the proximal area, the frond develops from a strong, rigid stem 1.0 mm. in diameter. This extends for some distance distally before it bifurcates in the upper medial part of the frond. The secondary branches in the same area extend laterally from the strong, axial stem in much the same manner as in *Ptylopora*. In the medial part of the frond, the branches assume their characteristic generic relations of large primaries and subordinate secondaries.

The primary branches are strong. They increase in width distally from 0.45 mm. to 0.65 mm. The secondaries increase in width from 0.26 mm. to 0.33 mm. The width of the fenestrules is about equal to the width of the secondary branches, the ratio generally being 1 to 1. The total variability of the number of secondary branches in 10 mm. is 12 to 17. Both the primary and secondary branches are sharply angular on the obverse side. The mesial carina is strong, broad, and rounded and has small, regularly spaced, conical nodes spaced approximately 0.36 mm. apart. The total variability of the number of nodes in 5 mm. is 9 to 15. The interapertural surface of the obverse side of the branches is smooth but slightly striated when weathered. The reverse side of the branches is sharply angular, subnodose, and strongly striated when weathered.

Dissepiments round, striated when weathered, and relatively strong. They expand in width on the reverse side where they measure 0.23 mm. to 0.26 mm. On the obverse side, they measure from 0.13 mm. to 0.23 mm. in width. They are strongly depressed below the level of the branches on both sides of the frond.

Fenestrules elongate-quadrate. They measure from 1.05 mm. to 1.55 mm. in length and 0.23 mm. in width. Total variability of fenestrules in 10 mm., 7 to 10.

Zooecial apertures small, circular. Average diameter 0.07 mm. They are spaced approximately two and one-half to three diameters apart longitudinally. The peristomes are not prominent. Total variability of zooecial apertures in 5 mm., 16 to 19.

Discussion.—The irregular development of the branches, and the smaller proportions clearly differentiate this species from *Ptiloporella laticrescens* Hall & Simpson which occurs in the Middle Devonian of Canada. However, in general appearance the two forms are comparable.

The meshwork pattern of *Ptiloporella varia* is interesting because it displays characteristics of three closely associated genera. The proximal part of the frond reminds one of *Ptylopora*. The medial part is distinctly characteristic of *Ptiloporella*, while the nearly uniform width of the branches in the distal part gives the frond the appearance of *Fenestella*. This arrangement suggests an evolutionary modification of the Devonian ptiloporellid stock inasmuch as forms of *Ptiloporella* have not been previously re-

ported from formations younger than the Devonian.

In regard to this development, it was extremely interesting to the author to find a notation by Ulrich of a form in the Waverly group at Richfield, Ohio, which he regarded as a variety of *Fenestella albida* Hall. He named this form *F. albida* var. *richfieldensis*, and described it (1888, p. 66) as being very similar to *F. albida* but differing as follows: "In the peculiarly irregular and lax growth of its fronds—the branches are also less straight and the fenestrules more variable in size and shape. In some of the specimens, a few branches are stronger than the rest, and the whole may assume an irregular pinnate arrangement—on the reverse, also the branches are usually narrowly rounded or subangular, a feature not noticed on typical examples of the species." Although Ulrich states that "this variety brings the species into close proximity with *Fenestella filistriata* Ulrich, a Burlington limestone species," it is obvious that the relationship is superficial, because the latter lacks not only the irregular pinnate arrangement of the branches but also the nodose keel, and it has a much coarser meshwork.

The relationship of *F. albida* var. *richfieldensis* and *Ptiloporella varia* is relatively close. The only difference is that the former has a slightly coarser meshwork and contains fewer nodes in 5 mm. on the obverse keel. It is feasible that the variety described by Ulrich represents the last vestiges of the ptiloporellid stock, inasmuch as he notes that only "in *some* of the specimens a few branches are stronger than the rest."

Occurrence.—Ptiloporella varia is found throughout the Chouteau group at localities 2 to 6.

Family ACANTHOCLADIIDAE Zittel, 1880
Genus PTYLOPORA McCoy, 1844
PTYLOPORA sp.
Pl. 22, fig. 5; Text-fig. 2b

Zoarium pinnate. Weak secondary branches extend laterally from the main stem at angles of approximately 60 to 80 degrees.

Main stem round, striated, and slightly flexuous. Its nearly constant width tapers gradually from 0.34 mm. in its lower portion to 0.32 mm. in its upper portion. The lateral branches, however, increase in width from their point of attachment outward. Near the main stem, they are 0.26 mm. wide, and they expand to a width of 0.31 mm. They are subangular and bear traces of regularly spaced nodes on the reverse side. These lateral branches are regularly arranged and spaced at intervals of 0.39 mm. to 0.45 mm. along the main stem, with 13 to 14 situated in the space of 10 mm.

The lateral branches are not normally supported by dissepiments, but one or two dissepiments may be present at a distance from the main stem. Occasionally, a short pinna will form the support of two lateral branches. The scattered dissepiments, which are depressed below the level of the branches on the reverse, are about 0.09 mm. in width and are situated about 1.2 mm. to 1.5 mm. from the main stem.

Discussion.—The above description is based upon the reverse side of a single specimen, and it is believed that this is insufficient for specific identification. The specimen does, however, bear a close resemblance to the form described and illustrated by Ulrich as *Pinnatopora subangulata* from the Cuyahoga shales of the Waverly series at Cuyahoga Falls, Ohio. Ulrich's description fails to mention the presence of dissepiments and small irregularly spaced nodes on the reverse of the secondary branches, but the fact that both these features are present can be seen in his illustration (Ulrich, 1888, pl. 14, fig. 2). These same features are also present in the Chouteau specimen. Another feature common to both forms is the subangular character of the reverse—a feature which Ulrich uses as a distinguishing feature for his species (Ulrich, 1888, p. 76). A minor difference between the two forms is that Ulrich's form usually has 12, sometimes 11 to 13 pinnae in 10 mm. along the midrib, whereas the Chouteau specimen has from 13 to 14 in the same distance. Additional material from the Chouteau group may prove these two forms to be conspecific.

Because the Chouteau specimen does possess dissepiments, the author believes that it should be considered as a *Ptylopora*, but Ulrich probably would have designated it as a *Pinnatopora* because of its close affinity to that genus and because of the relative scarcity of dissepiments. In his discussion of the

species *Pinnatopora intermedia* Ulrich, which somewhat resembles the Chouteau specimen, he makes the following statement (1888, p. 75):

> In having the longer lateral branches united by dissepiments this species approaches *Ptilopora*, but the general aspect and growth of the zoarium is so much like *Pinnatopora* that it has seemed advisable to place the species as above rather than under the former genus. If, however, possession of non-celliferous dissepiments is insisted upon as being the only point of difference between the two groups, then the species will have to stand as *Ptilopora intermedia*.

Again in the discussion of another similar species, *Pinnatopora simulatrix* Ulrich, he states (1888, p. 75) that:

> This is another species that simulates *Ptilopora* in having some of the longer lateral branches united by dissepiments. I am, however, inclined to hold that species of the type of this and the preceding ones cannot be removed from *Pinnatopora* if we propose to make natural affinity the primary disideratum of our classifications.

Occurrence.—Fragments resembling the above description of *Ptylopora* sp. are found throughout the Chouteau group at localities 3 to 5.

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POLYLOPIA CLARK, AN ORDOVICIAN SCAPHOPOD

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ABSTRACT—Restudy of the previously unassigned narrow conical genus *Polylopia* Clark discloses that it bears features which ally it most closely with the Scaphopoda. These are: (1) possession of a multi-layered wall, (2) presence of external longitudinal ribbing, and (3) truncation of the gradually tapering narrow cone. Characteristics diagnostic of other kinds of narrow conical shells as tentaculitids, styliolinids, hyolithids, conularids, pteropods, cephalopods, or worms are lacking and placement in any of these groups is not supported by the evidence at hand. The suggested placement of *Polylopia* in the Scaphopoda extends the stratigraphic range of this group in North America back to the Middle Ordovician.

INTRODUCTION

SCAPHOPODS, or tusk shells as they are customarily known, unlike other mollusks, are rare in Paleozoic strata, especially so in those of Early Paleozoic age. Eichwald (1856, 1860) described *Dentalium acus*, *D. notabile*, and *D. granosum* var. *laevigatum* from the Middle Ordovician Orthoceras limestone near Poulkovo, Russia, but their assignment to the Scaphopoda has been seriously questioned by Pilsbry & Sharp (1897–1898). As I have not seen these specimens or pictures of them, I cannot comment on the scaphopodan nature of these species. Over half a century has elapsed since the appearance of the most comprehensive review of fossil and living scaphopods (Pilsbry & Sharp, 1897–1898). Little else has been added to our knowledge of Paleozoic forms since then save for a handful of papers on Middle and Late Paleozoic forms (Girty, 1903; Hayasaka, 1925; Greger, 1933; Young, 1942; Miller, 1949). Failure to recognize additional species from Early Paleozoic rocks is probably due, in part, to lack of knowledge of scaphopodan ancestry and the difficulty of recognizing accepted scaphopodan features in the abundant but poorly known narrow conical shells of uncertain zoological affinities from the Lower Paleozoic rocks. It was fortunate, therefore, that I had the opportunity to examine many specimens of the unassigned *Salterella billingsi* Safford 1869, in the course of preparing the chapter on miscellaneous narrow conical shells of uncertain classificatory status for the *Treatise on Invertebrate Paleontology*. Detailed examination showed that the external and internal features of this species were strikingly like those of the well-known scaphopod *Dentalium*. The purpose of this paper is to provide additional information on the genus *Polylopia* and analyze the evidence supporting placement with the Scaphopods.

[1] Published by permission of the Assistant Commissioner, New York State Museum and Science Service, Journal Series No. 20.

GEOLOGIC SETTING

The specimens under consideration came from the Murfreesboro limestone (Central limestone of Safford, 1869, p. 259) of Middle Ordovician age. The Murfreesboro limestone is the lowest formation of the Mohawkian stage of the Champlainian Series in the Central Basin of Tennessee. This unit correlates approximately with the base of the Caradoc in Europe. The rock is light blue or "dove"-colored, fine-grained, very cherty limestone, heavily stained brown by iron oxide. A label, apparently in Safford's handwriting, on specimen USNM 15247 (originally numbered 714), denotes that these specimens came from along the C., St. L. & N. Railroad, 1 mile north of Murfreesboro, Tennessee.

The fossils are uniformly stained brown, always silicified, and exhibit no preferred orientation. Some bedding planes are replete with *Polylopia billingsi* (Safford), accompanied by lesser numbers of the gastropod *Lophospira medialis* (Ulrich and Scofield), the ostracode *Leperditia fabulites* (Conrad), and the pelecypod *Ctenodonta gibbercula* Salter, in that order.

All the figured specimens are in the U. S. National Museum with the catalogue number 15247.

SYSTEMATIC PALEONTOLOGY

PHYLUM MOLLUSCA

Class SCAPHOPODA Bronn, 1862

Family DENTALIIDAE Gray, 1847

Genus POLYLOPIA Clark, 1925

Type species: Salterella billingsi Safford, 1869.

POLYLOPIA BILLINGSI (Safford)

Pl. 23, figs. 1–10

Salterella billingsi Safford, 1869, Geology of Tenn., p. 289. *Polylopia billingsi* (Safford). Clark, 1925, Trans. Royal Soc. Canada, p. 12, pl. 1, figs. 1,2.

Description.—Safford's (1869, p. 289) original description is as follows: "From one and a half to two inches long, straight, large end of longest specimens about one-sixth of an inch in diameter, tapering to a point, striated longitudinally, cross-section circular. A beautiful and abundant species; at least three cones, one within the other."

Multi-layered, narrow conical shell, tapering very gradually but not terminating in a point. I disagree with Safford's observation on this matter. No specimen has been observed which retained a pointed apex. This implies that either no such condition existed or that fortuitously enough all apical points have been broken off. Openings at both ends of shell. Longitudinal riblets on exterior are distinct but less so than in the well-known scaphopod *Dentalium*. Furthermore, these riblets are more numerous than in that genus and consequently closer together, being 0.4 mm. apart on larger specimens and 0.25 mm. apart on smaller ones, tending to converge apically.

Whereas living scaphopods possess shells which are more or less gently curved, *Polylopia* is straight. This lack of curvature is the sole departure from generally accepted scaphopodan characteristics (some living scaphopoda are nearly straight). It is possible that Early Paleozoic scaphopods had not yet acquired a curved shell due to their mode of existence; no specimens of *Polylopia* were found penetrating bedding. Living scaphopods, on the other hand, assume an angle of 35–40 degrees with the sea bottom, the larger of the two openings, from which the "foot" emanates, being buried in the bottom deposits. Ordovician scaphopods may not have developed the burrowing habit of their descendants.

There is some variation in size but most of the specimens average 44 mm. in length and have apertural diameters of 3.5 mm. and apical diameters of 2 mm. One specimen attained 5.15 mm. in diameter; another has an apical diameter of only 0.5 mm. The length is more variable than the width, probably due to wear, breakage, and resorption of the shell material. Seemingly, the number of shell layers bore relationship to the rapidity with which the outermost layers were removed.

The central core is approximately one-half the total diameter and averages 1.8 mm. for all specimens examined. In some cross-sections, this core is excentric and may represent the position of the mantle cavity.

Longitudinal polished sections reveal that the number of shell layers is not constant. Several specimens show only one, others two, and some up to five layers; the majority have three of four layers. Gray and white layers alternate, the former are almost always the thicker. The white layer may actually be a fusion of two thin white layers as is suggested in a few weathered specimens. If this is correct, the inner part of the inside white layers may correspond to the thin structureless outer layer of living scaphopod shells (periostracum) which contains the sculpture of the shell, the thick gray layer may be the ostracum, and the very thin inner layer (fused with the next outer layer) is possibly the hypostracum. However, in some sections the gray and white layers are of about equal thickness. In one figured specimen (Pl. 23, fig. 6), each of the three layers present has a uniform thickness of 2.15 mm., the three invaginated cones having diameters of 2.72, 3.15, and 3.58 mm. Another longitudinal section (fig. 4) shows four layers, gray alternating with white, with gray layers averaging 0.47 mm. and white layers averaging 0.22 mm. A third specimen (fig. 3) contains gray layers 0.26 mm. thick and white layers just one-half this thickness. No noticeable thinning or thickening of layers occurs in individual specimens.

A few forms display markings which ap-

pear to be borings in the shell, possibly caused by rapacious gastropods, perhaps the ubiquitous *Lophospira medialis*.

CLASSIFICATORY STATUS

If scaphopods were not living today, it would be very difficult to demonstrate the molluscan affinities of these fossils for the shells, without soft parts, exhibit radial symmetry, a feature characteristic of several phyla. Furthermore, no other living mollusk known has a long slender shell open at both ends. In my opinion, the multi-layered shell, prominent longitudinal ribbing, and the presence of an apical opening in the narrow conical shell are regarded as sufficient criteria to relate *Polylopia* to the scaphopods. No other biologic group possess these features collectively. The degree of taper and size of *Polylopia* compares favorably with those of other Paleozoic conical shells but there, however, the similarity ceases. A multi-layered shell is not known among the tubicolar worms and the presence of longitudinal ribbing denies an assignment to the pteropods, tentaculitids, styliolinids, hyolithids, or conularids. Though *Polylopia* has a circular cross-section, it lacks any other tentaculitid traits such as the ubiquitous transverse annuli. From conularids, *Polylopia* differs in that it lacks quadri-radial symmetry and flexible periderm. Hyolithids are roughly trigonal in cross-section and have opercula, structures which have not been seen in specimens of *Polylopia*. There is no evidence of septa or an internal tube which could be construed as a siphuncle. Hence any relationship with the cephalopods or volborthellids is unsupported. I am in complete accord with Clark (1925) who refuted any relationship of this species with *Salterella*. Though we do not know to which zoologic group *Salterella* should be assigned, it is certainly not a scaphopod, since *Salterella* lacks recognized scaphopodan features.

Excepting the questionable scaphopods from the Orthoceras limestone of Russia, *Polylopia* ranks as the most ancient scaphopod known.

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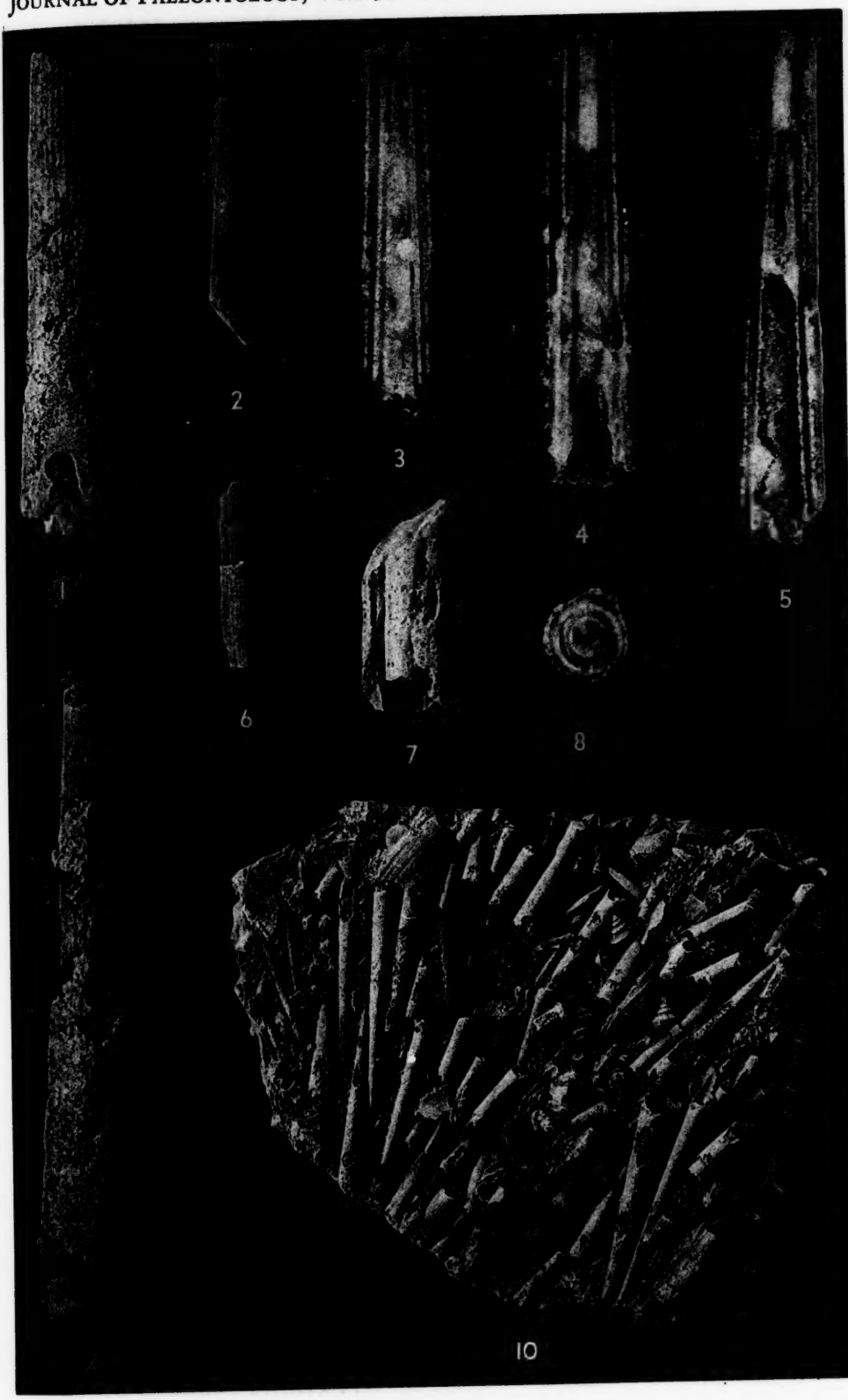
MANUSCRIPT RECEIVED MARCH 5, 1957

EXPLANATION OF PLATE 23

FIGS. *1–10—Polylopia billingsi* (Safford). *1*, exterior showing fine ribbing, ×4. *2*, apparent curving due to breakage, ×2. *3–5*, longitudinal polished sections showing layering, ×4. *6*, weathered specimen showing three layers, ×2. *7*, Weathered specimen showing internal core and ribbing on inside of shell. ×4. *8*, polished cross-section showing concentric layers. ×4. *9*, partly exfoliated specimen, ×4. *10*, Slab showing several good specimens of *Polylopia* associated with *Lophospira medialis* and *Ctenodonta gibbercula*, ×1.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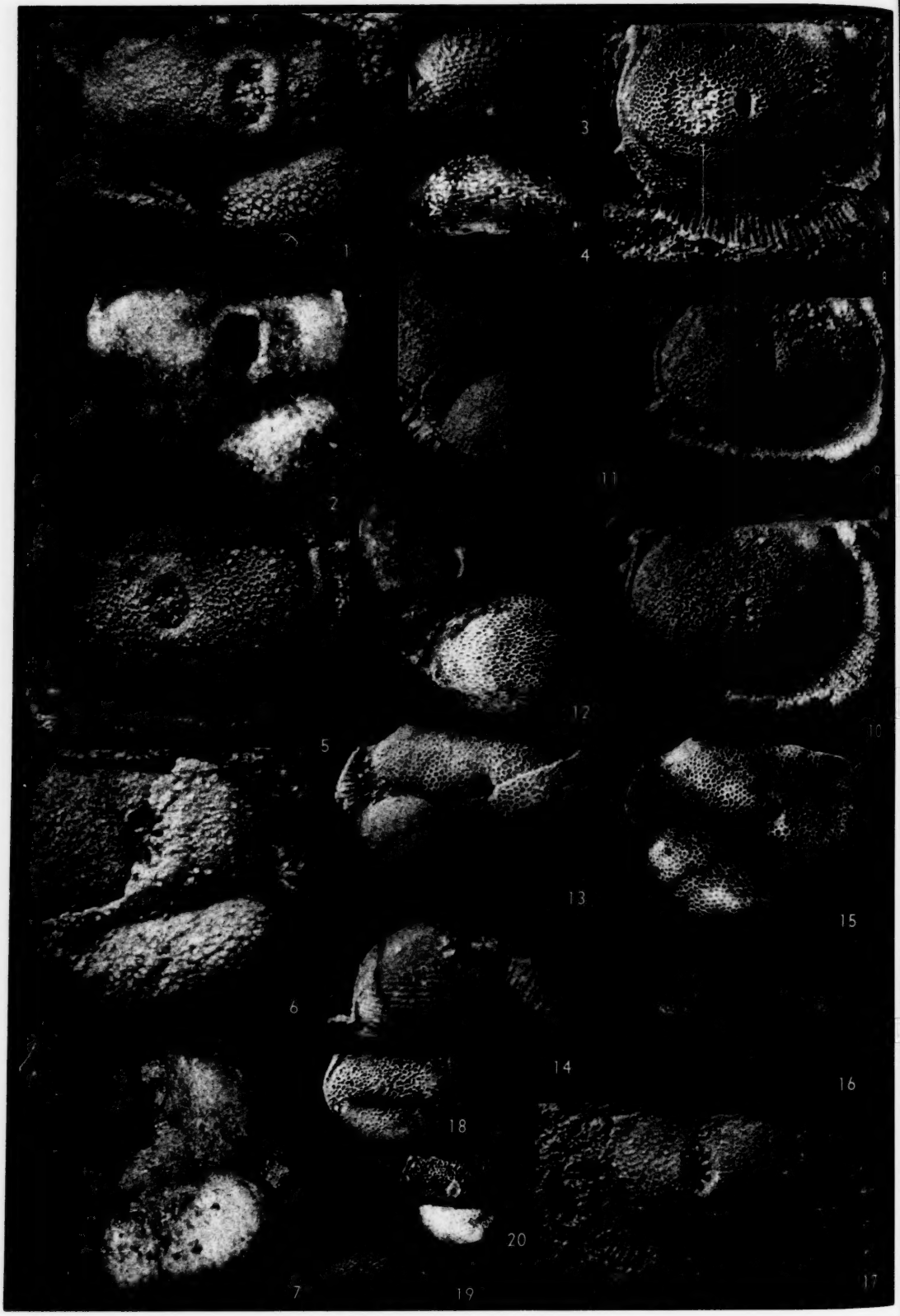
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JOURNAL OF PALEONTOLOGY, V. 32, NO. 1, P. 147–151, PL. 24, 7 TEXT-FIGS., JANUARY 1958

BOLBINEOSSIA, A NEW BEYRICHIID OSTRACOD GENUS

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ABSTRACT—The Silurian ostracods which Ulrich & Bassler (1923) assigned to the genus *Chilobolbina* are in neither the same genus nor the same family with *C. dentifera* (Bonnema), the type species. They are beyrichiids. We here establish for them the new genus *Bolbineossia*, type species *B. didictyosa*, n. sp.

Bolbineossia resembles *Chilobolbina* in having a nearly central pit and a broad frill from corner to corner, and in being dimorphic. Female ostracods of the two genera cannot be assigned to the correct genus on the basis of a lateral view. Despite their remarkable similarities, the two genera are not closely related. The female of *Bolbineossia* has a brood pouch (opening into the domicilium), whereas the female of *Chilobolbina* has a false pouch (outside of the domicilium).

INTRODUCTION

IN 1923, in the process of describing Silurian ostracods of Maryland, Ulrich & Bassler erected the genus *Chilobolbina*. There is no doubt about their intent. Obviously, they set up *Chilobolbina* as a genus to which could be assigned certain beyrichiid ostracods from the Silurian strata of Maryland and adjacent areas. They made one error. They selected as type species an ostracod known from the Middle Ordovician of Estonia, *Primitia dentifera* Bonnema. This error defeated their purpose. *Chilobolbina dentifera* is not a beyrichiid; it has a false pouch rather than a brood pouch.

As a result, *Chilobolbina* is a good genus, but it does not include beyrichiid ostracods such as Ulrich & Bassler assigned to it. To date, no genus has been established for the Silurian beyrichiid ostracods which superficially resemble *Chilobolbina*. We believe such a genus is necessary, and name it *Bolbineossia*.

We express our appreciation to Dr. G. Arthur Cooper, Dr. Remington Kellogg, and Dr. I. Gregory Sohn of the United States National Museum for the loan of specimens of *Chilobolbina dentifera* (Bonnema). We are also indebted to Dr. George M. Ehlers of the Museum of Paleontology, University of Michigan, for his help in collecting ostracods from the Silurian rocks of the Northern Peninsula of Michigan.

REVIEW OF *Chilobolbina*

Bonnema (1909, p. 25) described *Primitia dentifera* from the Middle Ordovician Kuckers formation in Estonia. This ostracod has a broad frill from corner to corner and a central pit. It is dimorphic. The female has a

EXPLANATION OF PLATE 24

(All figures ×30)

FIGS. *1–7,17—Chilobolbina dentifera* (Bonnema). Specimens catalogued together as USNM 58376. *1–4*, two lateral and two ventral views of female right valve; specimen uncoated in figs. 2 and 4; note that ammonium chloride emphasizes the ornamentation and configuration but obscures the denticles projecting into the central pit. *5*, lateral view of male left valve. *6,7*, two lateral views of incomplete female right valve; specimen uncoated in fig. 7 to show striations in false pouch. *17*, lateral view of immature left valve.

8–16—Bolbineossia didictyosa, n. sp. *8*, lateral view of male right valve, allotype, No. 33748. *9,10*, lateral views of two male right valves, paratypes, Nos. 33749 and 33750. *11,12*, lateral views of incomplete female right valve, paratype, No. 33751; fig. 12 uncoated to show ornamentation of brood pouch. *13–16*, two lateral and two ventral views of female left valve, holotype, No. 33752; specimen not coated in figs. 15 and 16.

18–20—Dolichoscapha escharota, n. sp. *18,19*, lateral and ventral views of female left valve, holotype, No. 34450. *20*, lateral view of same specimen without coating of ammonium chloride.

bulbous false pouch formed by part of the frill. Specimens of this ostracod are very fragile. Insofar as we know, no complete valve has ever been separated from the matrix, Kuckers shale (kuckersite). Specimens exposed on surfaces of the shale do not reveal the nature of the pouch. Only in thin sections, polished surfaces, or carefully exhumed parts of valves can the bulbous structure be proved to be a false pouch, lying outside the domicilium and opening below the contact margin.

In 1923, Ulrich & Bassler discovered some Silurian ostracods with a broad frill from corner to corner and a central pit in each valve. Females of these ostracods have a bulbous structure in the anteroventral region in a position corresponding to that described and illustrated by Bonnema for *Primitia dentifera*. The description given by Ulrich & Bassler (1923, p. 515) for *Chilobolbina* shows they intended that the genus should include dimorphic ostracods in which the female has a brood pouch:

"Carapace with the broad striated frill characteristic of the subfamily [Eurychilininae], a simple, short, more or less deeply impressed median furrow or spot, the median lobe barely elevated above general convexity of surface, the male closely resembling the older, simply sulcate section of *Eurychilina*. The female differs in having a prominent long ovate brood pouch that covers approximately the posterior three-fifths of the ventral part of the frill and laps slightly onto the convex part of the valve."

It is no discredit to Ulrich and Bassler that they chose a type species with a false pouch. It was not clear from the original figures and description that *Primitia dentifera* had a false pouch. Furthermore, their Silurian ostracods were embedded in a hard matrix, which obscured the ventral edge of the pouch. Actually, their description of the Silurian species as having brood pouches appears to have been fortunate conjecture, for none of the type specimens shows conclusively that the bulbous structure is a brood pouch, opening into the domicilium.

In brief, the genus *Chilobolbina* is valid, its authors are Ulrich & Bassler 1923, and its type species is *C. dentifera* (Bonnema) 1909. However, the Silurian species *C. punctata* U. & B., *C. punctata brevis* U. & B., *C. billingsi* (Jones), and *C. hartfordensis* U. & B. have brood pouches and are not congeneric with *C. dentifera* (Bonnema).

Öpik (1937, p. 22) was the first to determine that the pouch of *C. dentifera* was a false pouch.

Henningsmoen (1953, p. 227) discussed the classification of *Chilobolbina*. The most recent work is that of Jaanusson (1957, p. 233–241), who made *Chilobolbina* the type genus of the subfamily Chilobolbininae (family Eurychilinidae), carefully reviewed the characters of the genus, and described two new species.

Some additional illustrations and a few pertinent remarks about *Chilobolbina dentifera*, we think, will clarify the nature of the dimorphic frill. In the female, the part of the frill in the anterodorsal and anterior regions and the part in the posteroventral, posterior, and posterodorsal regions resemble those in the male. The anteroventral part of the frill, however, is bulbous and forms a false pouch which closes against the corresponding structure of the opposite valve. As pointed out by Jaanusson (1957, p. 235) this part of the frill is set onto the rest of the valve somewhat higher than the rest of the frill. The bulbous section is continuous with the rest of the frill; each of the two junctures of the bulbous section with the adjacent flat sections is sharply depressed as a deep fissure (pl. 24, figs. 1–4). We have based a reconstruction of the interior view of a female valve (text-fig. 3) on lateral, anterior, and ventral views of incomplete valves. There has been conjecture on the nature of the edges of the false pouch. Hessland (1949, p. 126) said, "The margins of the convex part of the velum seem to lie together when the carapace is closed." As can be seen in plate 24, figures 3–4, the periphery of the false pouch has a narrow, liplike margin. This margin appears to extend at least to the plane of the contact margin. We believe that the edges of the opposing false pouches formed a closure when the valves were drawn together.

Another point needs clarification. The ornamentation of the pouch in this species was described by Jaanusson (1957, p. 237) as follows: "The proximal narrow part of the dolon adjacent to the domicilium is radially striated. . . . The other parts of the dolon

are covered with moderately large, closely spaced tubercles which are much smaller and more numerous than in *C. sudermannica.*" We would add to this that the tubercles distally give way to striae parallel to the periphery (pl. 24, figs. 3,4).

We wish to point out, incidentally, that the central pit appears larger and the denticles within it more clearly defined in specimens that are not coated (compare pl. 24, figs. 1 and 2). This observation should be considered in evaluating photographs of *Chilobolbina* species taken with a coating of sublimate.

SYSTEMATIC DESCRIPTION

Order OSTRACODA

Superfamily BEYRICHIACEA

Family BEYRICHIIDAE

BOLBINEOSSIA, n. gen.

Type species.—*Bolbineossia didictyosa*, n. sp.

Diagnosis.—Beyrichiid ostracod with only a central pit (S2) to represent sulcation. Wide frill, in the female extending onto the protuberant brood pouch.

Description.—Only single valves available. Overlap and hingement not known. Hinge line straight. Valve subovate to subelliptical in lateral view. Domicilium subelliptical, evenly convex except for deep pit (S2) near the center. Frill broad, extending from corner to corner; in the female extending onto the brood pouch. Surface in known species reticulate.

Remarks.—*Bolbineossia didictyosa*, n. sp., was selected as type species because specimens are available to show definitely and distinctly the nature of the brood pouch. The Silurian species assigned to *Chilobolbina* by Ulrich & Bassler (1923) also belong to this genus: *B. punctata* (U. & B.), *B. punctata* brevis (U. & B.), *B. billingsi* (Jones), and *B. hartfordensis* (U. & B.)

Henningsmoen (1953, p. 227) suggested, "These species [Silurian species assigned by Ulrich & Bassler (1923) to *Chilobolbina*] may be transferred to *Apatobolbina*, which will then include forms with or without sulcal pit." We believe the differences in lobation in beyrichiid ostracods are generic. We regard *Bolbineossia* and *Apatobolbina* as distinct genera.

Bolbineossia is the only beyrichiid with a nearly central pit as the only sulcation; it is readily distinguished from all other genera of the family by this character. The female of *B. didictyosa*, the type species, has the frill encroaching onto the ends of the pouch but not extending across it; however, the females of *B. hartfordensis* and *B. punctata*, according to Ulrich & Bassler's illustrations (1923, pl. 37, figs. 7,11), have frills extending completely across their brood pouches.

The name of the genus is derived from Greek *βολβωδης* ("bulbous") and *νεοσσια*, f. ("nesting place") and refers to the shape and function of the brood pouch.

Geologic range.—Only Middle Silurian species are known.

BOLBINEOSSIA DIDICTYOSA, n. sp.

Pl. 24, figs. 8–16; text-figs. 5–7

"*Chilobolbina*" sp. Kesling, 1957, pl. 4, figs. 4–6. Kesling & Rogers, 1957, p. 1000, pl. 127, figs. 10–14.

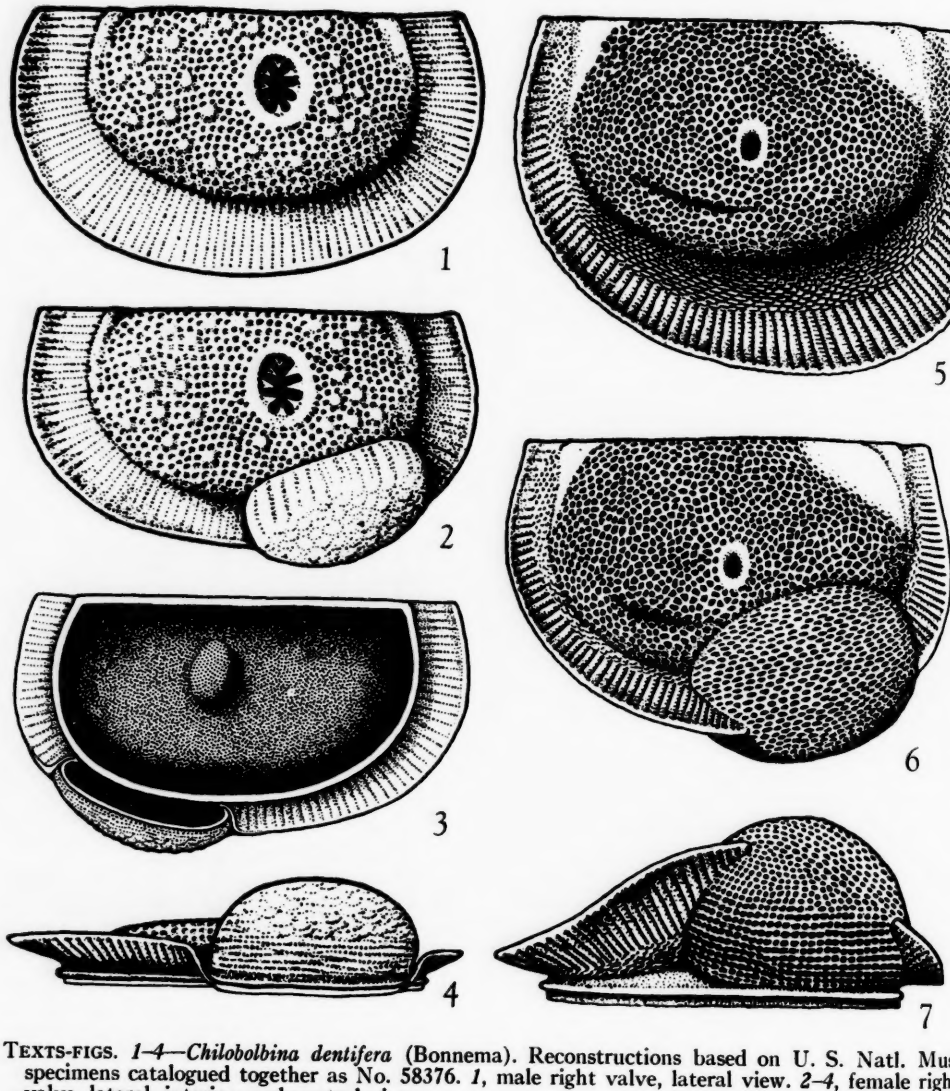
Diagnosis.—A species of *Bolbineossia* with a very broad frill. Frill ornamented with two distinct kinds of ornamentation, proximal flat-ended papillae and distal striae. Ventral part of brood pouch in the female ornamented with rectangular reticules arranged in rows.

Description.—Hinge line straight. Domicilium subelliptical as seen in lateral view, its height about three-fifths its length. Corners of domicilium protuberant. Central pit deep, its diameter equal to about 1/20th the length of the domicilium. Corner areas of domicilium set off from the rest of the lateral surface by distinct curved grooves. Narrow groove on posteroventral region of lateral surface, more or less parallel to the ventral edge of the domicilium, about one-third as long as the domicilium, its front end below the pit about midway between the pit and the frill.

Male with broad frill from corner to corner, widest in the anteroventral region, where its width is greater than half the height of the domicilium.

Female with a bulbous ovate brood pouch on the anteroventral part of the lateral surface. Brood pouch about two-thirds as long as domicilium. Frill encroaching onto each end of the pouch, but not crossing it.

Submarginal ridge in each dimorph; in



TEXTS-FIGS. *1–4—Chilobolbina dentifera* (Bonnema). Reconstructions based on U. S. Natl. Mus. specimens catalogued together as No. 58376. *1*, male right valve, lateral view. *2–4*, female right valve, lateral, interior, and ventral views.

TEXT-FIGS. *5–7—Bolbineossia didictyosa*, n. sp. Reconstructions based on University of Michigan, Museum of Paleontology, Nos. 33748–33752. *5*, male right valve, lateral view. *6,7*, female right valve, lateral and ventral views.

the female, part of it adjacent to the brood pouch.

Lateral surface finely but distinctly reticulate except narrow posterodorsal corner area, large anterodorsal corner area, and narrow ring around the pit, all of which are smooth. Reticules on lateral surface more or less polygonal, arranged without apparent pattern. Reticules on lateral surface of brood pouch elongate parallel to long axis of pouch; those on ventral surface of brood pouch square, arrayed in straight rows parallel to the free edge of the valve.

Frill with two distinct kinds of ornamentation: proximal papillae and distal striae. Papillae elongate, subrectangular, more or less in concentric rows. Distal striae deep, faint concentric lines between striae. As seen

on broken specimens, the striae lie between tubules inside the frill. These tubules now filled with clear calcite, but probably hollow originally. Tubules extend, as seen in broken frill, into the proximal (papillose) part of the frill.

Remarks.—*Bolbineossia didictyosa*, n. sp., differs from *B. hartfordensis* (Ulrich & Bassler) in having a narrow curved groove posteroventral to the pit and an anteroventral brood pouch (rather than a centroventral). It differs from *B. punctata* (Ulrich & Bassler) and *B. punctata brevis* (U. & B.) in having distinct ornamentation on the brood pouch. *B. billingsi* (Jones) seems to have, according to Ulrich & Bassler's figures (1923, pl. 37, figs. 4–6), a narrower frill, larger smooth ring around the pit, only one kind of ornamentation on the frill, and a groove which extends not only across the posteroventral region but also onto the anteroventral region. Ulrich & Bassler's retouched figures show that the frill extends across the pouch in *B. hartfordensis* (1923, pl. 37, fig. 7) and *B. punctata* (pl. 37, fig. 11); they do not mention the relationship of frill and brood pouch in their descriptions (1923, p. 516, 520).

The trivial name is derived from Greek δι- ("double, two") and δικτυον, n. ("network") and refers to the two kinds of reticulation on the brood pouch.

Types.—Holotype, a female left valve, No. 33752. Allotype, a male right valve, No. 33748. Paratypes, two male right valves, Nos. 33749 and 33750, and a female right valve, No. 33751.

Occurrence.—All specimens are from a thin, irregular, discontinuous layer of chert exposed in the abandoned White Marble Lime Company quarry in the city of Manistique, Schoolcraft County, Michigan. This layer, at most 1/16 inch thick, is at or near the top of the Middle Silurian Schoolcraft dolomite of the Manistique group.

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JOURNAL OF PALEONTOLOGY, V. 32, NO. 1, P. 152–153, PL. 24, 1 TEXT-FIG., JANUARY 1958

DOLICHOSCAPHA, A NEW BEYRICHIID OSTRACOD GENUS

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ABSTRACT—A very small ostracod from the Middle Silurian Schoolcraft dolomite of Michigan is a female beyrichiid characterized by a smooth central spot, reticulate lateral surface, elongate ventral brood pouch, and a prominent velate ridge. It has no sulci. It is classified as *Dolichoscapha escharota*, n. gen. and n. sp.

Order OSTRACODA
Superfamily BEYRICHIACEA
Family BEYRICHIIDAE
DOLICHOSCAPHA, n. gen.

Type species.—*Dolichoscapha escharota*, n. sp.

Description.—Only a female left valve of the type species known. Male, overlap, and hinge unknown. Hinge line long and straight. Valve nonsulcate, reticulate except for a central smooth spot. Velate ridge extending to each corner. Brood pouch ventral, elongate.

Remarks.—*Dolichoscapha* has a unique combination of features which are known singly in other genera. It resembles *Mesomphalus* Ulrich & Bassler 1913 in having an elongate ventral brood pouch, but differs from that genus in being nonsulcate and reticulate. It has a velate ridge similar to that in *Bolbiprimitia* Kay 1940, but it has a more protuberant and distinct brood pouch and lacks an S2. Unlike the smooth *Apatobolbina* Ulrich & Bassler 1923 and *Phlyctiscapha* Kesling 1953, which are also nonsulcate, the new genus is reticulate; furthermore, its elongate brood pouch is sharply defined, not posteriorly confluent with the lateral surface like that in *Phlyctiscapha*, and its velate structure is a ridge, not a frill like that in *Apatobolbina*. Although *Dolichoscapha* has reticulation like that in *Bolbineossia* Kesling, Heany, Kauffman, & Oden 1958 (described in the preceding article), it has a more elongate and more nearly ventral pouch and has a central smooth area instead of a pit.

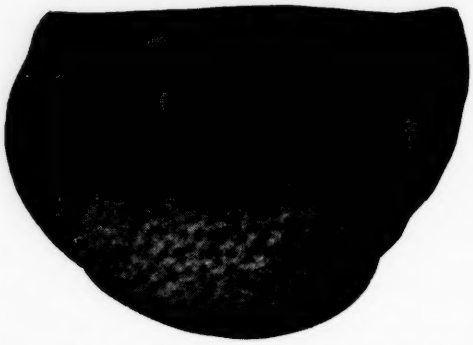
The central smooth spot is very similar to that in species of *Platybolbina* Henningsmoen 1953, a genus of the subfamily Chilobolbininae according to the classification of Jaanusson (1957, p. 233). In particular, the central smooth spot of *Dolichoscapha escharota*, the type species, resembles that of *Platybolbina kapteyni* (Bonnema) (see Jaanusson, 1957, pl. 4, figs. 1–3). It undoubtedly marks externally the position of the internal adductor-muscle scar.

Briefly, we can describe this genus as having an *Apatobolbina*-like lobation, a *Platybolbina*-like central smooth spot, a *Mesomphalus*-like brood pouch, a *Bolbineossia*-like reticulation, and a *Bolbiprimitia*-like velate ridge.

The name of the genus is derived from Greek δολιχος ("long") and σκαφη, f. ("a cradle") and refers to the shape and function of the brood pouch.

DOLICHOSCAPHA ESCHAROTA, n. sp.
Pl. 24, figs. 18–20; Text-fig. 1

Description.—Dorsal border very gently arched, extending slightly above the hinge line. Valve with a distinct swing. H/L ratio about 2/3. Central smooth spot subpyriform in outline, about $\frac{1}{3}$ as high as valve. Brood pouch ventral, elongate, its length about $\frac{2}{3}$ of that of the valve, its height about $\frac{2}{5}$ that of the valve. Velate ridge, round-edged, slightly protuberant above the hinge



TEXT-FIG. 1—*Dolichoscapha escharota*, n. sp. Lateral view of holotype, a female left valve. ×85.

line at the corners, extending ventral to the brood pouch. Whether the ridge is complete or separated into two parts below the brood pouch is not clear. Submarginal ridge parallel to free edge, in lateral view obscured by velate ridge.

Lateral surface reticulate, with reticules of several sizes, apparently without regular arrangment except, perhaps, that those on the periphery of the central spot are large and those anterodorsal to the spot are small. Brood pouch ornamented with faint reticulation, much shallower than that on the lateral surface.

Dimensions of holotype, a female left valve: length, 0.73 mm.; height, 0.48 mm.; and width, 0.30 mm.

Remarks.—Inasmuch as this is the only species known in the genus, it is impossible to say whether it is unusually small. It is well known that species of beyrichiid ostracods vary greatly in size within the same genus, so that other species of *Dolichoscapha* may be found which are larger than this very small ostracod.

The name of the species is derived from Greek εσχαρα,f. ("scab, a scar from a burn") and refers to the central smooth spot.

Type.—Holotype, a female left valve, catalogued and deposited in the Museum of Paleontology of the University of Michigan as No. 34450.

Occurrence.—The holotype and only specimen is from a thin, irregular, and discontinuous layer of chert exposed in the abandoned White Marble Lime Company quarry in the city of Manistique, Schoolcraft County, Michigan. This layer, at most $\frac{1}{16}$ inch thick, is at or near the top of the Middle Silurian Schoolcraft dolomite of the Manistique group.

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JOURNAL OF PALEONTOLOGY, V. 32, NO. 1, P. 154–170, PLS. 25,26, 7 TEXT-FIGS., JANUARY 1958

MORPHOLOGY AND ONTOGENY OF A LOWER CAMBRIAN PTYCHOPARIOID TRILOBITE FROM NEVADA*

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ABSTRACT—Detailed description of the morphology and ontogeny of a micropygous ptychoparioid trilobite, *Crassifimbra walcotti* (Resser), is presented, based on excellently preserved silicified material, including some complete specimens, from the Early Cambrian Combined Metals member of the Pioche shale at Pioche, Nevada.

Statistical investigation of 100 meraspid and holaspid cranidia from one locality shows a maximum of 20% variation in selected cranidial dimensions. Slight but significant differences in these dimensions between apparently contemporaneous populations at localities 4 or more miles apart are interpreted as possible examples of infraspecific geographic variation.

Five developmental stages are recognized: I, anaprotaspid, with a subcircular outline, a pair of short posterior marginal spines, an undivided glabella extending nearly the full length of the shield, a continuous marginal border, a hypostome with eight posterior marginal spines, a rostrum, free cheeks, and a proparian facial suture; II, metaprotaspid, with a distinct protopygidium and ocular lobes, and no posterior marginal spines, otherwise like the anaprotaspid; III, early meraspid, with the glabella extending to the anterior margin, hypostome with poorly defined marginal spines, free cheeks reaching to the genal angles, gonatoparian facial sutures, up to at least three thoracic segments, and a transitory pygidium about ⅔ the size of the cephalon; IV, middle meraspid, with the glabella separated from the anterior margin by a border only, a hypostome without marginal spines, free cheeks with short genal spines, opisthoparian facial sutures, between 4 and 9 thoracic segments, and a transitory pygidium about ½ the size of the cephalon; and V, late meraspid and holaspid, with both brim and border between the unfurrowed (exclusive of occipital furrow), anteriorly tapered glabella and the anterior margin, anterior border furrow generally with strong median inbend posteriorly directed and 10 or more thoracic segments. Meraspid specimens have a slightly more parallel sided glabella than holaspid specimens but otherwise have the same morphology.

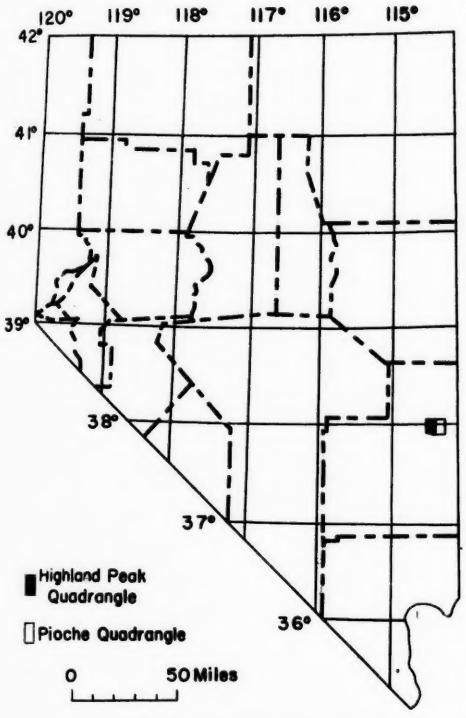
INTRODUCTION

GENERALIZED trilobites usually referred to as ptychoparioid are among the most abundant forms in the Cambrian rocks of the United States. These trilobites provide one of the most perplexing and challenging taxonomic problems in Cambrian paleontology. In this group where knowledge of the complete trilobite is often necessary for proper identification, it is extremely difficult to obtain either complete individuals or enough disarticulated parts of individuals to gain a proper understanding of the morphology or variation in morphology of the whole trilobite. Thus, for most of the Cambrian ptychoparioid trilobites, morphology and morphologic variability are inadequately known and attempts at grouping these trilobites into recognizable genera and higher taxonomic categories reflect this lack of knowledge. Almost nothing is known of the early developmental stages of these forms—knowledge that might have an important bearing on their classification and relationships.

The discovery by C. W. Merriam in 1949 of a fauna of abundant, well-preserved silicified Lower Cambrian trilobites including two olenellids, *Olenellus gilberti* Meek and *Paedeumias clarki* Resser, and a ptychoparioid, *Crassifimbra walcotti* (Resser), in the Pioche district, Nevada (text-fig. 1) has provided an unparalleled opportunity for obtaining full understanding of the morphology and ontogenetic development of these species. The ontogeny of *O. gilberti* and *P. clarki* has already been described (Palmer, 1957). This paper presents the results of an investigation of the morphology and ontogeny of *C. walcotti* and seeks to establish a firm basis for the future development of a ptychoparioid phylogeny.

The holotype of *C. walcotti* was collected

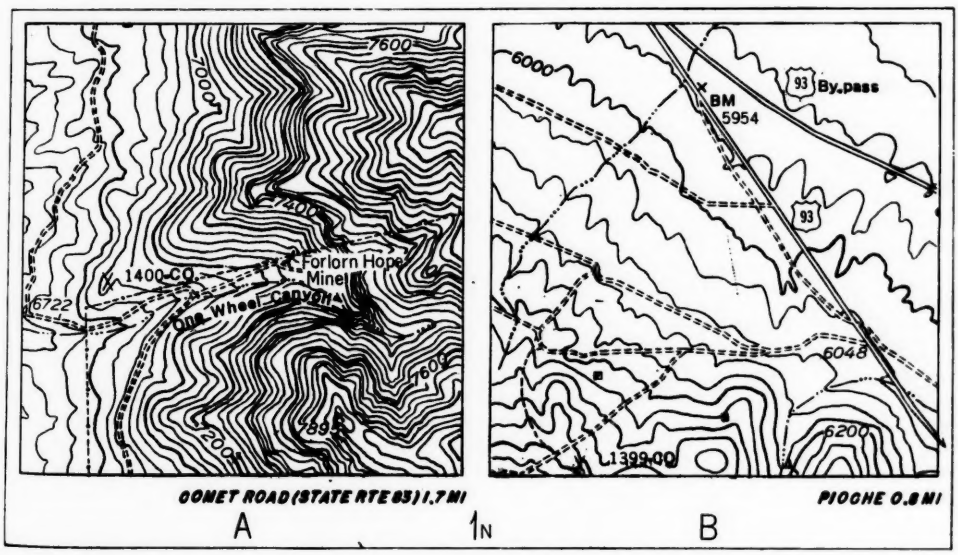
* Publication authorized by the Director, U. S. Geological Survey.



TEXT-FIG. *1*—Map of Nevada showing location of Highland Peak and Pioche quadrangles covering the Pioche district.

at USGS locality 30, 8 miles north of Bennett's Spring on the west side of the Highland Range, about 10 miles west of Pioche, by C. D. Walcott, 1885. This locality is probably in the vicinity of Lyndon Gulch, about 4 miles south of locality 1400-CO described below. Although the trilobites in the type lot are not silicified, it is assumed on the basis of known distribution of Early Cambrian ptychoparioid trilobites in the Pioche shale that they came from beds approximately contemporaneous with those at localities 1399-CO and 1400-CO (text-fig. 6). The specimens are preserved in gray medium-grained crystalline limestone and provide information, particularly with regard to surface details, that is not available from the silicified specimens.

Silicified specimens identified here as *C. walcotti* are known to be present at two localities in the upper few feet of the so-called Combined Metals bed of the Pioche shale in the Pioche district, Nevada (text-fig. 2): (1) USGS locality 1399-CO, at West End prospect, elevation about 6390, SE¼-SW¼SW¼ sec. 16, T. 1. N., R. 67 E, Pioche quadrangle, Nevada, about 1.6 miles WNW of Pioche, collected by C. W. Merriam, 1949; (2) USGS locality 1400-CO, on NW face of SW directed spur, elevation about



TEXT-FIG. *2*—Maps showing localities in the Pioche district, Nevada from which silicified Early Cambrian trilobites have been obtained. A. sec. 29, T 1 N, R 66 E. Highland Peak quadrangle. B. sec. 16, T. 1 N, R. 67 E. Pioche quadrangle.

6840. NE¼NW¼SW¼ sec. 29, T. 1 N., R. 66 E., Highland Peak quadrangle, Nevada, about 1.8 miles NNE of the Comet mine on the west side of the Highland Range, collected by C. W. Merriam and A. R. Palmer, 1953. At these localities, silicified trilobites are present throughout a unit of fine-grained medium-bedded blue-black limestone up to six feet thick. The quality of the specimens from locality 1400-CO is better than that of specimens at locality 1399-CO. Most of the observations and conclusions presented in this paper were derived from the study of specimens from locality 1400-CO.

METHODS AND PROCEDURES

Silicified specimens were obtained for study by preparing insoluble residues of the fossiliferous limestone. Solution of the limestone in dilute formic acid left a residue made up almost entirely of trilobite material. The residue was then decanted from the initial dissolving vessel into an 80- or 100-mesh sieve submerged in a basin of water, thus keeping breakage to a minimum. After thorough soaking in at least one change of water, the residue was dried on the sieve.

The dry silicified specimens are remarkably sturdy. After larger specimens were removed directly from the sieve to shallow trays, the remaining material was poured onto a clean sheet of paper. Small quantities of this material were then scattered on a black metal plate and searched at about 30× with a binocular microscope. Well-preserved specimens were transferred with a fine (00) brush from the metal plate to cardboard microslides and subsequently sorted for detailed study.

Drawings were prepared by examining specimens at appropriate magnifications using an ocular grid, and transferring the images to graph paper. Most specimens that were to be drawn in dorsal or ventral aspect were mounted in cardboard microslides; small specimens to be viewed in profile were mounted on the heads of insect pins; and large specimens were mounted on cardboard points through which insect pins were then inserted, a procedure in common use by entomologists. The specimens on insect pins were oriented under the microscope by inserting the pins in an appropriate position in plasticene. All specimens were whitened with a light coating of magnesium oxide for study. This coating can be removed by a drop of any dilute acid.

The drawings on figures 3–5,7 were prepared as pencil sketches by me and inked by Mrs. Elinor Stromberg. The photographs were prepared by Mr. N. W. Shupe.

Measurement of specimens for statistical analysis was made under a binocular microscope at 30× with a micrometer eyepiece permitting reading to 20ths of a millimeter (1 division = 0.05 mm). Regressions and subordinate statistics were computed following Shaw (1956). Comparison of regressions was made according to Imbrie (1956, p. 235–238). The statistical data, regression lines and limits of variability including 95% of the population are plotted on text-figure 6.

MORPHOLOGY

The descriptive terminology used here is essentially that used by Whittington & Evitt (1954, p. 11–14). In addition, the term frontal area is applied to the region between the front of the glabella and the anterior margin. This can be divided by the anterior border furrow into a border (anterior) and a brim (posterior). The abbreviated terms sagittal (sag.) and transverse (tr.) are used as qualifiers indicating a direction either in the axial line or at right angles to it respectively, when statements of length and breadth might otherwise be ambiguous. The terminology for cephalic sutures is discussed below under "Cephalic sutures." Suggestions for modification of the definitions of anaprotaspid and metaprotaspid developmental stages are given below under the heading "Ontogeny."

The holotype of *C. walcotti* (pl. 25, fig. 1), from USGS locality 30, although showing the external surface, is unfortunately not an example of the characteristic appearance of cranidia of this species. The two anterior pairs of glabellar furrows are rather prominent and the posteriorly directed median inbend in the anterior border furrow is not well developed. However, it is the only specimen with these characteristics in a large collection where there are many associated cranidia that are essentially identical to it in form and size. These specimens lack

the well developed anterior glabellar furrows and have a prominent posteriorly directed median inbend in the anterior border furrow (pl. 25, figs. 2,3). The sum of the characteristics of all of these cranidia is considered to present a more representative picture of the appearance of the cranidium of *C. walcotti*. As thus understood, individual cranidia of *C. walcotti* from the type locality cannot be consistently distinguished from cranidia at USGS localities 1399-CO and 1400-CO (cf. pl. 25, figs. 2,4,10) and they are all considered here to represent the same species. Information for the following description was derived almost entirely from the excellently preserved silicified material at USGS locality 1400-CO.

SYSTEMATIC DESCRIPTION

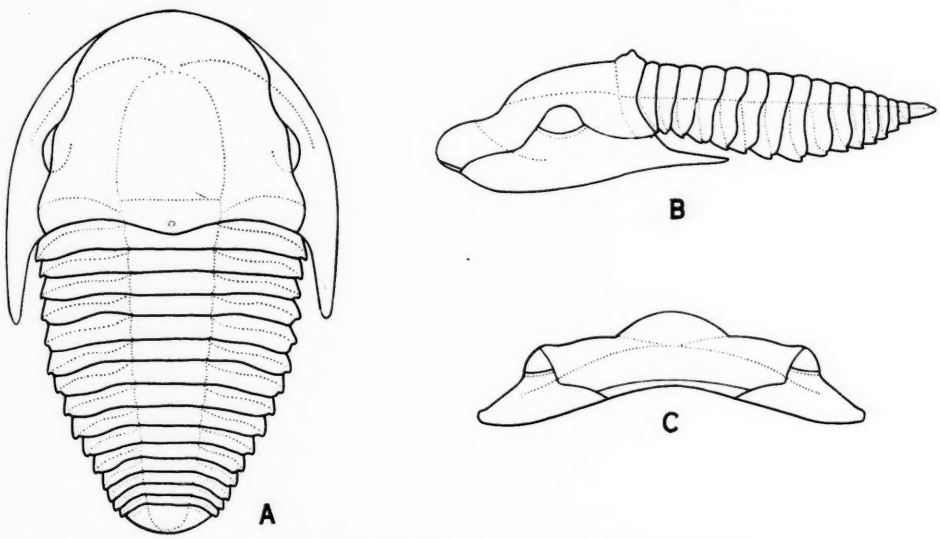
Genus CRASSIFIMBRA Lochman, 1947
CRASSIFIMBRA WALCOTTI (Resser)

Pl. 25, figs. 1–4, 7–25; pl. 26, figs. 1–24; Text-figs. 3–7

Onchocephalus walcotti Resser, 1937, p. 21.
Crassifimbra walcotti (Resser), Lochman, 1947, p. 64,71, text-figs. 1–3.

Crassifimbra walcotti (Resser) is a small trilobite that probably rarely exceeded 15 mm. in axial length. Its exoskeleton (text-fig. 3A) is elongate subovate in outline, broadest opposite the occipital ring, and micropygous. The cephalon has a semiparabolic dorsal outline, and a straight posterior margin between genal spines whose tips extend straight posteriorly to the level of the fourth thoracic segment. In profile (text-fig. 3B; pl. 25, fig. 7) the greatest depth of the cephalon is beneath the occipital ring. In anterior view (text-fig. 3C; pl. 25, fig. 8) the border is arched upward.

The cranidium is subtrapezoidal in outline, moderately arched transversely and longitudinally, and has its greatest width across the posterior limbs. The glabella tapers forward slightly and decreases in height until it merges nearly imperceptibly with the frontal area. Axial furrows are well defined only along the sides of the glabella. They are deepest at the occipital ring and become shallow and are usually not apparent anterior to the position of junction of the eye ridge with the glabella. Only some of the largest silicified cranidia (5 to 6 mm. in axial length) (pl. 25, fig. 11) have indications of glabellar furrows and of eye ridges. Three pairs of shallow furrows, exclusive of the occipital furrow, may be discerned. The occipital furrow has a nearly constant depth in all but the largest cranidia where some specimens show a distinct shallowing on the



TEXT-FIG. 3—Reconstruction of *Crassifimbra walcotti* (Resser), approximately ×5. A. dorsal view; B. left lateral view; C. anterior view.

axial line. The occipital ring bears a small median node.

The outline of the glabella, and the positions of the galbellar furrows and eye lines are much better developed on the under side of the cranidium (pl. 25, fig. 15) than on the external surface (pl. 25, fig. 10).

The frontal area is dominated by a broad, strongly arched border with a prominent median posterior directed extension that reaches nearly to the front of the glabella. The marginal furrow is broad and shallow and appears to merge with the axial furrow at the anterior end of the glabella, dividing the brim into two laterally expanding areas. The junction of the axial and marginal furrows is marked by a shallow depression directly in front of the glabella. In profile (pl. 25, fig. 7), the border is strongly and evenly arched, with its inner portion nearly horizontal and its marginal portion nearly vertical. The junction with the rostrum is slightly submarginal.

The fixed cheeks have a gently arched profile in anterior view (pl. 25, fig. 8) and the palpebral lobes are depressed slightly below the level of the axial furrows. The palpebral lobes are differentiated from the remainder of the cheek by an abrupt change in slope of the cheek surface. Although there is no palpebral furrow in the sense of a linear depression outlining the palpebral lobe, the posterior part of the lobe is better defined than the anterior portion which, on many specimens merges nearly imperceptibly with the cheek.

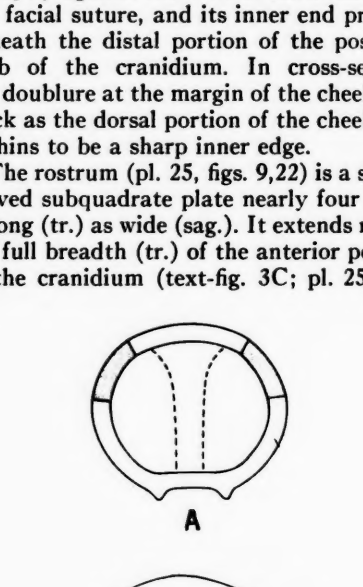
The posterior limbs are short (tr.) and blunt. A moderately deep straight posterior border furrow extends to the lateral margin of the limb but does not pass onto the free cheek.

In ventral view, the cranidium has a doublure only along the posterior margin beneath the distal portions of the posterior limbs and beneath the occipital ring (pl. 25, fig. 15). The anterior margins of the doublures in these three areas lie on a straight line passing through the juncture of the axial furrow with the posterior margin of the cranidium. At the distal ends of the doublure beneath the posterior limb, a thin short point projects anteriorly.

The free cheeks (pl. 25, figs. 9,16–18) are slender, their greatest width is about one-fifth of their length. The anterolateral margin is moderately curved and the posterolateral margin is nearly straight. A border is not differentiated on the outer surface although a slight break in the slope of the anterior portion of the cheek indicates the approximate position of the lateral border furrow. The genal spine is about one-third the length of the cheek.

In ventral view (pl. 25, fig. 18) the inner end of the anterior portion of the doublure is broader than the portion beneath the lateral margin of the cheek. It projects inward for a short distance beneath the border of the cranidium and terminates abruptly against the rostrum. Posteriorly, the doublure ends abruptly against the ventral continuation of the facial suture, and its inner end projects beneath the distal portion of the posterior limb of the cranidium. In cross-section, the doublure at the margin of the cheek is as thick as the dorsal portion of the cheek, but it thins to be a sharp inner edge.

The rostrum (pl. 25, figs. 9,22) is a simple curved subquadrate plate nearly four times as long (tr.) as wide (sag.). It extends nearly the full breadth (tr.) of the anterior portion of the cranidium (text-fig. 3C; pl. 25, figs.



TEXT-FIG. 4—Reconstruction of ventral aspect of an anaprotaspid (A) and of an adult cephalon (B). Free cheeks shaded.

8–10). Its anterior margin is turned up abruptly nearly at right angles to the remainder of the plate. The posterior margin has a short posterior projection that is approximately but not always exactly median in position. The cross section (sag.) of the rostrum is identical to that of the doublure of the free cheek, so that the rostrum has a sharp posterior margin. The lateral and anterior margins are the same thickness as adjacent portions of the exoskeleton from which they are separated by sutures. The exterior surface of the rostrum has fine terrace lines comparable to those on the doublure of the cheeks.

The size of the rostrum with relation to the cranidium may be a critical character in determining the relationship of *C. walcotti* to other trilobites. In *Agraulos ceticephalus* (Barrande) which has a cranidium superficially similar to that of *C. walcotti*, the length of the rostrum (tr.) is only about half of the breadth of the anterior portion of the cranidium.

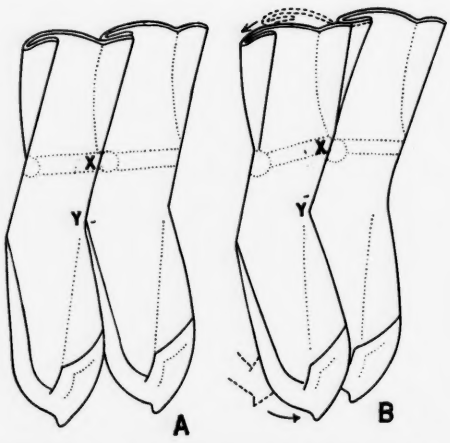
The hypostome (pl. 25, figs. 12–14) is small relative to the cephalon (text-fig. 7). It is elongate subquadrate in outline with a strongly rounded posterior margin, a sinuous anterior margin, and prominent, slender, blunt-tipped anterior wings. The breadth at the anterior wings is almost equal to the axial length. The breadth of the main body of the hypostome is about two-thirds of the axial length. In profile (pl. 25, fig. 14) the surface of the hypostome is gently arched longitudinally and moderately arched transversely. In exterior view (pl. 25, fig. 13), a poorly defined narrow border is present along the lateral and anterior margins. In interior view (pl. 25, fig. 12), a narrow doublure is present below the border. A pair of prominent projections extend dorsally about one-third of the length of the hypostome from the posterior end. These are apparently homologous with the posterior wings of Ordovician cheirurid hypostomes (Whittington & Evitt, 1954, p. 12, pl. 11, fig. 10) and many other trilobites.

Between the posterior wings the doublure has a narrow marginal groove. All of the adult hypostomes observed, and many assignable to middle meraspid or later stages have a large hole with irregular margins in the middle of the anterior portion. This may represent either an uncalcified area or a thin portion of the test that was not silicified.

The thorax is composed of at least 15 segments. The outer parts of the pleurae are bent sharply downward (pl. 25, fig. 25), the inner parts horizontal, and the breadth at the fifteenth segment is about three-eighths of the breadth at the first segment. In oblique posterolateral view (pl. 25, fig. 19; text-fig. 3B), the margins of the thorax appear to "belly" downward due to the relatively greater lengths of the outer parts of the middle thoracic segments. Each segment has a prominent pleural furrow that extends nearly to the tip, but otherwise is slightly different from adjacent segments in size and form (pl. 25, figs. 20,21).

The approximate position of isolated thoracic segments within the thorax can be determined by observing on each segment the form of the axial ring, the comparative lengths of the distal and proximal parts of each pleuron, the nature of the pleural tip, and the amount of posterior deflection of the distal part. The anterior segments (pl. 25, fig. 20) have a relatively longer articulating half-ring than the middle and posterior segments due to the posterior expansion of the occipital ring (text-fig. 3B). They also seem to be proportionately narrower than the more posterior segments. The distal part of each pleuron is about equal in length (tr.) to the proximal portion, and it is deflected moderately to strongly backwards. There is no distinct spine at the tip of the segment. The middle segments (pl. 25, figs. 21,25), have a less prominent articulating half-ring, the distal portion of each pleuron is distinctly longer than the proximal portion and not deflected posteriorly, and a short pleural spine is present at the tip of the segment. The posterior segments are similar to the middle segments except for the fact that the distal parts of each pleuron are about the same length (tr.) as the proximal parts.

In ventral view, each segment has a doublure beneath the posterior portion of the axial ring that is comparable with the doublure beneath the occipital ring on the cranidium. At the posterior margin, beneath the dorsal furrow, is a low rounded boss that appears to be a poorly developed appendifer. The doublure of each pleuron extends dis-



TEXT-FIG. 5—Internal oblique views of the left halves of two adjacent thoracic segments under normal (A) and enrolled (B) conditions. XY—articulating margin.

tally as a gradually widening band from the posterior margin at the fulcrum, around the tip and inward for a short distance along the anterior margin (pl. 25, fig. 24). Opposite the short terminal spine, the anterior portion of the doublure is displaced away from the dorsal surface of the segment along a transverse (tr.) line. In front of this line the doublure also extends noticeably further inward. This displacement of the anterior portion of the doublure provides a buttress against which the next posterior segment rests when the trilobite is enrolled (text-fig. 5), thus providing the trilobite with a means of maintaining tension in an enrolled position without pulling itself apart. There are no definite ball and socket joints along the margins of the pleura about which the segments can pivot during enrollment (pl. 25, figs. 21,25). However, the segments fit tightly together along the margins of the proximal (horizontal) portions of the pleura (XY, text-fig. 5) and use these margins as hinges for enrolling.

The pygidium (pl. 26, figs. 17–24) is subovate in outline and about two to two and one-half times as broad as long. In posterior view (pl. 26, fig. 24) the margins rise towards the rear and form an inverted V on the axial line. The only distinct furrows on the dorsal surface of all adult pygidia are the first pair of pleural furrows. Some specimens also show the first ring furrow and the second pair of pleural furrows (cf. pl. 26, figs. 18,19). The axial lobe is defined only by its slight elevation above the pleural lobes. In ventral view (pl. 26, fig. 20) it extends three-fourths

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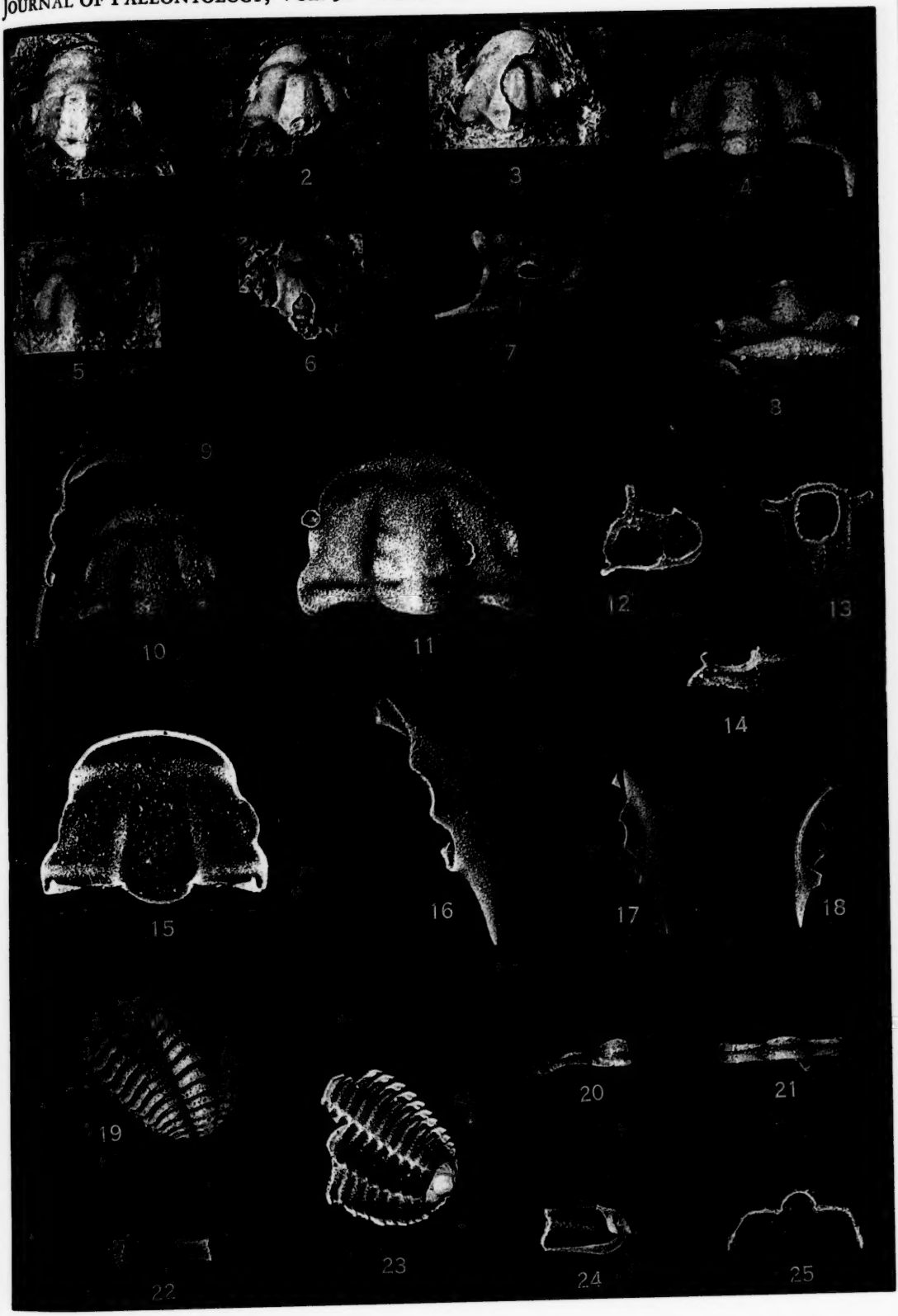
EXPLANATION OF PLATE 25

FIGS. *1–4,7–24—Crassifimbra walcotti* (Resser). *1*, holotype, dorsal view, ×5, USNM 61641 (Lochman, 1947, figs. 1,2). *2*, dorsal view of more characteristic appearing cranidium from type lot, ×5, USNM 61642a (Lochman, 1947, fig. 3). *3*, dorsal view, partly exfoliated cranidium from type lot, ×5, USNM 61642b. *4,7,8*, dorsal, lateral and anterior views of partly rebuilt cephalon, ×5, USNM 133202a. *9*, free cheek and attached rostrum showing internal aspect of rostrum, ×5, USNM 133202b. *10*, dorsal view of cranidium, ×5, USNM 133227. *11*, dorsal view of large cranidium showing shallow glabellar furrows. Note metaprotaspid of *C. walcotti* on left palpebral lobe, ×5, USNM 133202c. *12–14*, internal oblique, external and left lateral views of adult hypostome, ×10, USNM 133202d. *15*, ventral view of adult cranidium ×8, USNM 133202e. *16,17*, right free cheek: *16*, oblique view showing suture surfaces ×8; *17*, external view, ×5, USNM 133202f. *18*, ventral view, right free cheek, ×5, USNM 133202g. *19,23*, external and internal oblique views of adult thorax bearing fifteen thoracic segments and a pygidium, ×5, USNM 133203a. *20*, dorsal view, anterior thoracic segment, ×5, USNM 133203b. *21,25*, dorsal and anterior views, middle thoracic segment, ×5, USNM 133203c. *22*, external view, rostrum, ×5, USNM 133202h. *24*, internal view, distal portion of middle thoracic segment, ×10, USNM 133203d.

5—Onchocephalus thia (Walcott). Well preserved cranidium from type lot, ×5, USNM 64388.

6—Onchocephalus parvus (Walcott). Well preserved cranidium, dorsal view, ×5, USNM 133204.

Localities: Figures 1-3, USGS loc. 30, Pioche shale, 8 miles north of Bennetts Spring, Highland Range, Nevada; figure 5, USGS loc. 35h, Mt. Whyte formation, Mt. Bosworth, British Columbia; figure 6, USGS loc. 839-CO, Pioche shale, near top of spur, east side of Cave Canyon, elev. about 8510, Eureka District, Nevada; figures 4,7–25, USGS loc. 1400-CO, Pioche shale, NE¼ NW¼ SW¼ sec. 29, T. 1N, R66E, Highland Peak quadrangle, Nevada; figure 10, USGS loc. 1399-CO, Pioche shale, SE¼ SW¼ SW¼ sec. 16, T. 1N, R67E, Pioche quadrangle, Nevada.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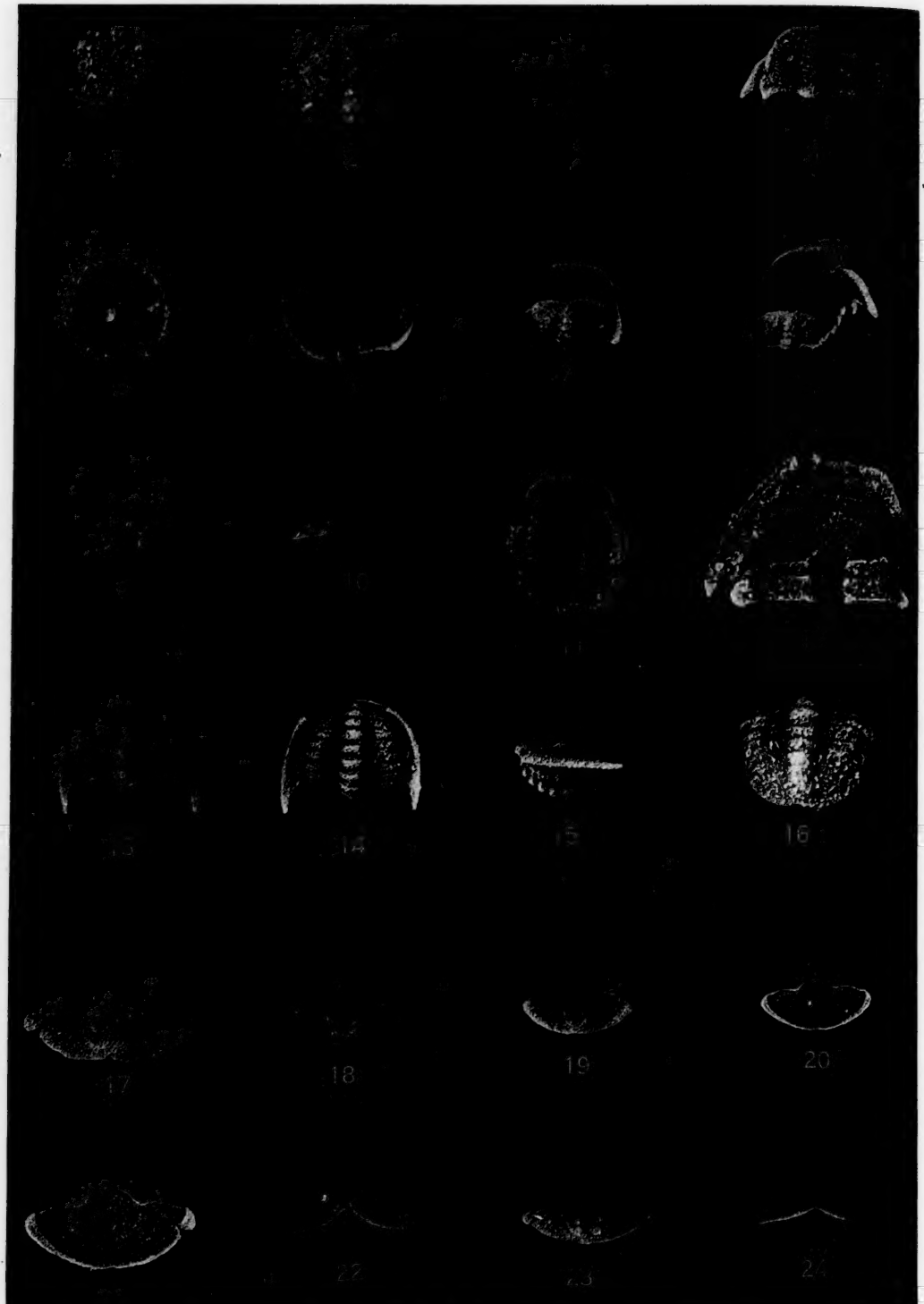
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or more the length of the pygidium. A narrow doublure, widest at the anterolateral corners of the pygidium, is present along the lateral margins. It tapers backwards and is absent immediately behind the axial lobe. As a result, the transverse convexity of the pygidium is often increased by post-mortem bending along the axial line where there is no doublure to strengthen the margin (cf. pl. 26, figs. 22,24).

Several specimens show variation in the release of thoracic segments to the thorax. One (pl. 26, fig. 23) has the pleural portions of a thoracic segment developed while the axial portion of the segment is still fused to the axial lobe. Another (pl. 26, figs. 17,21) has the pleuron of a thoracic segment developed only on the left side. The ventral view of this specimen (pl. 26, fig. 21) shows a doublure characteristic of a normal thoracic segment on the developed tip and a normal pygidial doublure on the opposite side. The absence of a pygidial doublure behind the developing thoracic segment may indicate that this is a pathologic specimen perhaps resulting from some injury sustained during life.

CEPHALIC SUTURES

Open sutures isolate the free cheeks and rostrum of *C. walcotti* from the cranidium and from each other. On adult specimens, the traces of these sutures appear as smooth surfaces at high angles to the test. The terms facial, rostral and connective sutures have been used for the sutures separating the free cheeks from the cranidium, the rostrum from the cranidium, and the rostrum from the free cheeks, respectively (Stubblefield, 1936). Rasetti (1952, p. 886) discusses cephalic sutures in Cambrian trilobites and rejects the term rostral suture. He believes that this suture is continuous with the facial suture, and that the term is "arbitrary and does not fulfill any descriptive or interpretative purpose." Certainly, from dorsal aspect of the cranidium of *C. walcotti*, Rasetti's objection appears acceptable. However, the ventral view (pl. 25, fig. 15) shows that the suture separating the rostrum from the cranidium meets the suture separating the free cheek from the cranidium at a distinct angle. The connective sutures, on the other hand, which Rasetti apparently accepts, seem to be merely continuations of the facial sutures across the doublure (pl. 25, fig. 16). These observations would seem to support a view opposite to that of Rasetti's. However, they are only true for the adult cephalon. The anaprotaspid (text-figs. 4A,7) shows the condition that Rasetti describes. A single approximately marginal suture separates the anterior portion of the doublure from the protaspid shield. A pair of transverse

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EXPLANATION OF PLATE 26

FIGS. *1–23—Crassifimbra walcotti* (Resser). *1,5,9*, anaprotaspid; *1*, dorsal view, USNM 133205a; *5*, ventral view showing hypostome, USNM 133205b; *9*, ventral view showing doublure, USNM 133205c; all ×30. *2,6,10*, metaprotaspid; *2*, dorsal view, USNM 133205d; *6*, ventral view showing cheeks, hypostome and rostrum, USNM 133205e; *10*, left lateral view, USNM 133205f; all ×30. *3,7,11*, early meraspid; *3*, dorsal view, USNM 133205g; *7*, ventral view of enrolled specimen showing cheek and transitory pygidium, USNM 133205h; *11*, ventral view of specimen showing hypostome and cheeks, USNM 133205k; note absence of genal spines; all figures ×20. *4,8,12*, middle meraspid; *4,8*, dorsal and ventral views of articulated specimen with seven thoracic segments, ×10, USNM 133205m; *12*, ventral view of cranidium with attached cheek, hypostome, rostrum and two thoracic segments, ×20, USNM 133205n. *13–15*, late meraspid; dorsal, ventral, and lateral views of enrolled specimen with 10 thoracic segments, 133205p. *16*, transitory pygidium with 2 attached thoracic segments, ×20, USNM 133203e. *17,21*, dorsal and ventral views of adult pygidium with thoracic segment developed on left side only, ×8, USNM 133203f. *18*, dorsal view of large adult pygidium with two pleural grooves, ×5, USNM 133203g. *19, 20,24*, dorsal, ventral and posterior views of normal adult pygidium, ×8, USNM 133203h. *22*, posterior view of slightly deformed adult pygidium, ×8, USNM 133203k. *23*, dorsal view of adult pygidium with incompletely formed thoracic segment fused at axis, ×8, USNM 133203m.

All specimens from USGS locality 1400-CO.

sutures divides this portion of the doublure into three subequal parts that are homologous with the free cheeks and the rostrum of the adult (text-fig. 4B). Thus the apparent continuation of the facial and connective sutures in the adult may be a secondary relationship and the primary morphologic relation of the rostral suture to the facial suture may be shown by ontogeny. Nevertheless, descriptive terms are an aid to clear communication of ideas. In adult specimens of *C. walcotti*, the rostral suture is a distinct entity and usage of the term in this paper fulfills a descriptive purpose. The terms facial suture and connective suture are used here for the portions of the longitudinal cephalic sutures separating the free cheeks from the remainder of the cranidium on the dorsal and ventral surfaces respectively. The facial sutures may be divided into anterior and posterior branches at the eye lobe. Neither the margin of the palpebral lobe nor the margin of the free cheek that bounds the lower surface of the eye show any indication of sutural surfaces. In both of these areas the test is noticeably thinner than elsewhere on the cephalon (pl. 25, figs. 15,16).

ATTACHMENT OF THE HYPOSTOME

There is no evidence in adults of *C. walcotti* for direct contact of the hypostome with other parts of the cephalon. The anterior margin of the hypostome, which is sinuous in adult forms (pl. 25, fig. 13) has a low marginal flange. The posterior margin of the rostrum to which it might attach has a thin edge comparable to the inner edge of the doublure of the free cheek. There are no opposing suture surfaces between the hypostome and the rostrum comparable to those between the rostrum and other parts of the cephalon. In immature forms, the rostrum and hypostome appear to have been in contact (pl. 26, fig. 6) but the pieces are so tiny that details of the contact cannot be ascertained. Certainly in the adult the hypostome and rostrum do not seem to have been connected by exoskeleton. If the hypostome always lies below the anterior portion of the glabella as suggested by Rasetti (1952, p. 891), then in *C. walcotti* it has probably retreated well back from the cephalic border. This might also explain why the hypostome and rostrum are in apparent contact in immature forms where the glabella reaches to the anterior margin of the cephalon.

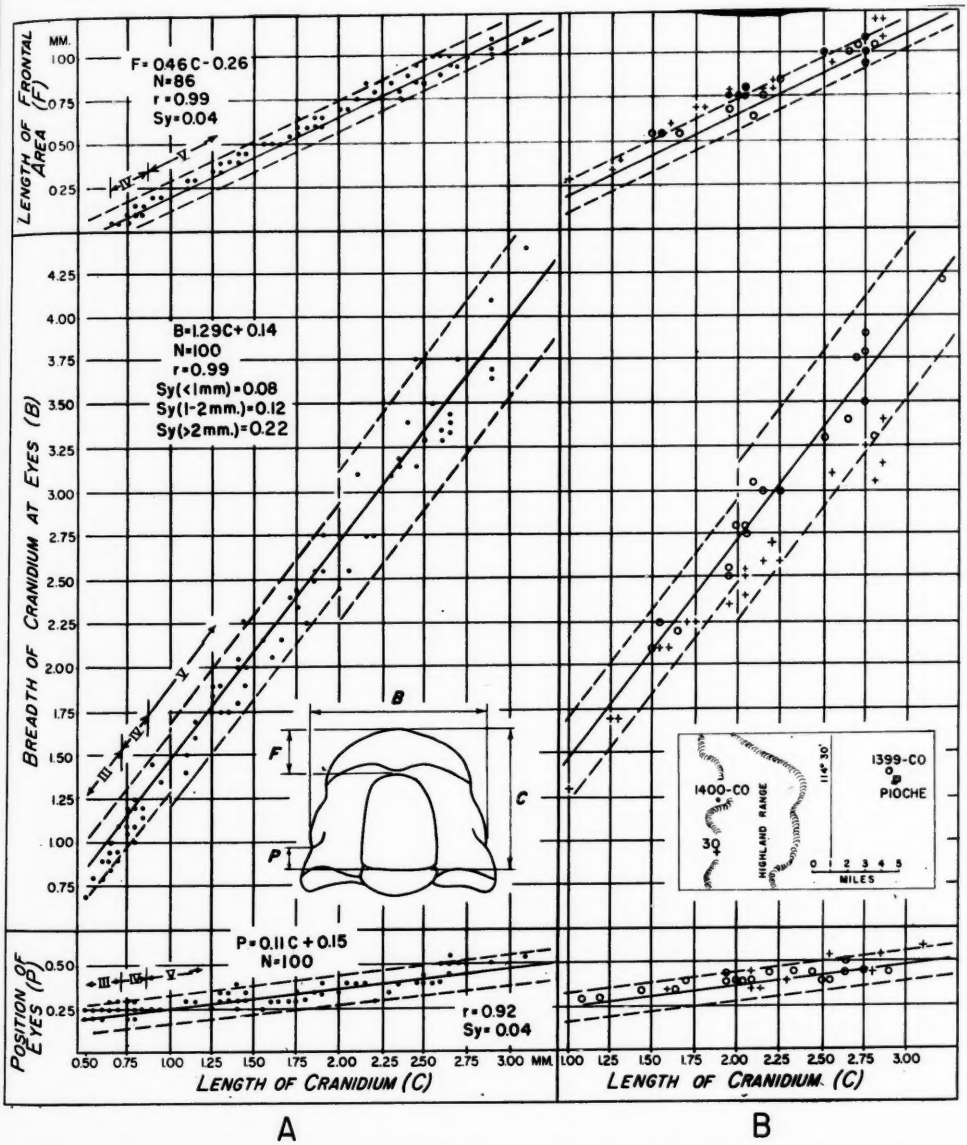
Although the anterior wings have blunt terminations and a suggestion of a low wing process (pl. 25, fig. 13) homologous to that of cheirurid hypostomes (Whittington & Evitt, 1954, p. 12, fig. 2), there are no indications of opposing points on the ventral side of the test with which the hypostome might have had direct contact. Perhaps the hypostome was never attached directly to any part of the cephalon in the adult, but was supported by attachment to the ventral membrane and by muscles as suggested for the Ordovician trilobite *Dimeropyge virginiensis* (Whittington & Evitt, op. cit., p. 40).

ADULT VARIABILITY WITHIN *C. walcotti*

Three types of differences have been observed between specimens of *C. walcotti:* (1) observable differences between individuals at one locality and between individuals from different localities, due to preservation; (2) measurable differences between individuals at one locality due to intrapopulation variation; and (3) measurable differences between individuals from different localities due either to geographic variability or slight differences in geologic age.

The most striking difference of the first type is between specimens retaining their test and internal molds (pl. 25, figs. 2,3). The test of *C. walcotti* is considerably thicker than that of the associated olenellid trilobites so that, while all features on the smooth external surface are subdued, those on the internal mold, such as the galbella are prominent. On some specimens, the cheek and brim of internal molds are punctate. This is one of the features of the monotypic genus *Sombrerella* (Lochman, 1948) from beds of late Early Cambrian age in northwestern Mexico. The two specimens representing *S. mexicana* Lochman are internal molds showing a prominent glabella and punctate cheeks and brim. They can only be compared with internal molds of other specimens and, in terms of features necessary for accurate identification, neither the genus nor the species is recognizable.

Differences of the second type are more subtle (text-fig. 6A). Several selected di-



TEXT-FIG. 6—Variation within *C. walcotti* (Resser). A. Variation within a paleontologic population, USGS loc. 1400-CO. B. Variation between populations at different localities. The index map shows the approximate geographic relations of the localities. The regression lines and 2 Sy limits are for the population at locality 1400-CO. +—shows dimensions of *C. walcotti* from USGS locality 30. 0—shows dimensions of specimens of *C. walcotti* from USGS locality 1399-CO.

mensions were measured on 100 cranidia of all sizes from locality 1400-CO. Three dimensions, the sagittal length of the frontal area, the breadth of the cranidium at the palpebral lobes, and the sagittal distance from a line connecting the posterior tips of the palpebral lobes to the occipital furrow were compared with the sagittal length of the cranidium measured forward from the occipital furrow. Regressions and standard de-

viations (S_y) were calculated for each pair of observations. Because of the increase in variability of the breadth of the cranidium with increasing size of the cranidium, S_y was computed for three size groups in this comparison (text-fig. 6A). The $\pm 2S_y$ limits indicated by dashed lines on figure 6 encompass 95% of the specimens within the population. For specimens with any selected cranidial length, there may be as much as 20% variation (10% to either side of the mean) in the breadth of the cranidium, the length of the frontal area, or the position of the posterior tips of the palpebral lobes with respect to the occipital furrow. Although this may seem to be considerable variation, the comparative dimensions of specimens from 60% of the population vary less than 5% ($\pm S_y$) to either side of the mean for particular cranidial lengths.

Variation in degree of distinctness of surface features has been noted in the description of the adult of *C. walcotti*. This variation involves changes in depth of the occipital furrow on the axial line and presence or absence of observable glabellar furrows or eye lines, principally on the largest cranidia. In general, the form of specimens from each locality is reasonably constant and the distinctiveness of dorsal and marginal furrows is remarkably constant. The external surface of all specimens is smooth.

Apparent geographic differences are shown on text-figure 6B. Specimens from localities 30 and 1399-CO, have cephalic furrow and surface characteristics essentially identical with those of specimens from locality 1400-CO. However, the length of the frontal area of specimens from locality 1399-CO, and both the length of the frontal area and breadth of the cranidium of specimens from locality 30 differ slightly and significantly from specimens at locality 1400-CO. In the absence of any consistent observable difference other than proportion, and because the proportional differences even though significant are small and not invariably sufficient alone for clear separation of any two specimens from two different localities, the statistical differences are considered here to be examples of geographic variation within a species. However, until detailed microstratigraphy within the Pioche shale can demonstrate absolute synchroneity of the three collecting horizons, the possibility that these statistical differences are due to slight differences in geologic age cannot be ruled out.

SYSTEMATIC POSITION OF *C. walcotti* (RESSER)

The problems of classification of Lower Cambrian ptychoparioid trilobites have been discussed by Lochman (1947, p. 59) and Rasetti (1951, p. 199–200; 1955, p. 4–9). These problems result from two principal facts: (1) practically all Lower Cambrian ptychoparioid trilobites are represented only by cranidia; and (2) few collections contain enough individual cranidia of a single species to determine the nature and limits of its morphologic variability.

The existing classification, which involves about 15 genera is developed entirely on similarities and differences of cranidia. Most of these Lower Cambrian genera lack definitive identifying characteristics and different paleontologists have placed different emphases on features considered by others to be of most critical importance for the recognition of a genus. For example, Lochman (1947) and Rasetti (1955) each present comparative analyses of the generic characteristics of *Antagmus* and *Onchocephalus*, but Rasetti places in *Onchocephalus* a species described by Lochman (1952) as *Antagmus solitarius*.

A possible complicating factor that has not been emphasized in the classification of ptychoparioid trilobites is homeomorphy of cranidia. Such homeomorphy has already been demonstrated by Rasetti (1951) in the Dolichometopidae. Additional examples are shown in the Corynexochidae, especially *Kootenia*, *Olenoides* and *Dorypyge*, and in some of the Upper Cambrian ptychoparioid genera assignable to the Pterocephaliidae such as *Labiostria* and *Litocephalus* (Palmer, 1954, 1956).

All of the factors mentioned above make the real relationships of *C. walcotti* to other Lower Cambrian ptychoparioids difficult to ascertain. Three described trilobite cranidia closely resemble those of *C. walcotti*. These are: *Onchocephalus parvus* (Walcott) (pl. 25, fig. 6) represented by two poorly preserved cranidia including the holotype which is a distorted internal mold; *Onchocephalus thia* (Walcott) (pl. 25, fig. 5) represented by three cranidia in the type lot, two of which,

including the holotype, are internal molds; and *Crassifimbra* sp. undet. 2 (Rasetti, 1955, pl. 2, fig. 10) represented by a single well preserved specimen.

Crassifimbra sp. undet. 2 differs from *O. thia*, *O. parvus* and *C. walcotti* by having a granular surface but is otherwise identical to *C. walcotti*. The latter three species all have shallow dorsal and marginal furrows, a poorly defined front to the glabella, and a smooth surface. *O. thia* appears to differ from *O. parvus* and *C. walcotti* in the more lateral direction of the posterior portion of the facial suture and longer distal portions of the posterior limbs. *O. parvus* could be conspecific with *C. walcotti* but it is represented by such poor material that such a synonymy is not warranted at this time. Although cranidia of these four species could be considered congeneric, such a combination would only indicate a different emphasis than those of Lochman and Rasetti on features that are believed to be of generic value. Such new combinations of cranidia into genera will not contribute greatly to our understanding of Lower Cambrian ptychoparioid trilobites. The real need in the taxonomy of these trilobites is for more information regarding the whole trilobite. Until such information is available, a satisfactory classification cannot be devised.

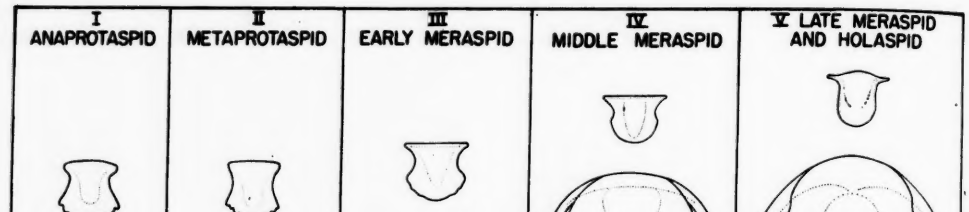
ONTOGENY

Most non-olenellid and non-agnostid trilobites apparently go through three distinct periods of development: the protaspid period when the dorsal covering of the larva is a single shield; the meraspid period when the dorsal covering of the immature trilobite includes a cephalon, transitory pygidium and range of thoracic segments from none to one less than the adult number; and the holaspid period when the dorsal covering of the trilobite includes a cephalon, pygidium and the full adult complement of thoracic segments.

The two stages of the protaspid period termed anaprotaspid and metaprotaspid have been defined by Størmer (1942, p. 56) as: (1) anaprotaspid—that stage in which the protaspid axis has only five segments, the most posterior of which is the occipital segment; and (2) metaprotaspid—that stage in which segments have been added posterior to the occipital segment. There is some evidence that the anaprotaspid axis may have more than four segments anterior to the occipital segment. Also, some species, such as *C. walcotti* have an unsegmented axis in the protaspid. Nevertheless, the morphologic position of the posterior part of the occipital ring is nearly always apparent. The anaprotaspid stage might thus be less equivocally defined as the stage in which the dorsal exoskeleton is a single shield showing no evidence of segmentation or of a distinct protopygidium posterior to the occipital ring. According to this definition and to Størmer's definition of the metaprotaspid stage given above, these stages seem to be valid and identifiable subdivisions of the protaspid period for most non-olenellid and non-agnostid trilobites.

The meraspid period has been divided by Størmer and others into numbered degrees, with the number corresponding to the total of free thoracic segments present. In the material of *C. walcotti*, less than one percent of the meraspid and holaspid specimens are complete. Assignment of disarticulated parts to particular meraspid degrees is not always possible. The same holds true for the holaspid period. For these reasons, three stages, characterized by morphologic development of the cranidium, are proposed here to include specimens in the meraspid and holaspid periods. In the *early meraspid stage*, the glabella is continuous with the eye ridge and reaches to the anterior margin of the cranidium; in the *middle meraspid stage*, the glabella is separated from the border by a frontal area composed only of the brim; and in the *late meraspid and holaspid stage*, the frontal area is divided by a shallow marginal furrow onto a brim and border. These stages are recognizable in the development of most known non-olenellid and non-agnostid adult trilobites with a brim and border. In the following discussion and the accompanying illustrations (text-fig. 7) the five developmental stages of *C. walcotti* are referred to by roman numerals as follows: I—anaprotaspid; II—metaprotaspid; III—early meraspid; IV—middle meraspid; V—late meraspid and holaspid. Developmental characteristics of the cephalon are summarized in Table 1.

Stage I (Anaprotaspid): (text-fig. 7; pl. 26, figs. 1,5,9). This stage is represented by 48 individuals averaging about 0.40 mm. in



TEXT-FIG. 7—Ontogenetic development of *Crassifimbra walcotti* (Resser). Length of glabella exclusive of the occipital ring is about equal for the dorsal and profile drawings. Hypostomes are in correct proportion to the corresponding dorsal views.

axial length. Twelve of the individuals retain a hypostome, two have a hypostome and rostrum, and one has hypostome, rostrum and cheeks, all slightly displaced.

The exoskeleton is subcircular in outline, gently arched transversely and longitudinally and bears a pair of closely spaced spines along the posterior margin.

In dorsal aspect (pl. 26, fig. 1) a narrow glabella extends nearly the entire length of the shield, expanding anteriorly and merging with a continuous marginal border. Similar complete borders appear to be present on a protaspid of *Olenus transversus* Westergard illustrated by Kaufmann (1933, Abb. 3, St. 2) and on a protaspid of *Strenuella gripi* Kautsky (Kautsky, 1945, pl. 16, fig. 3). Ružiča (1943, p. 28, pl. 4, figs. 7,8) shows a nearly complete marginal border for the anaprotaspid of *Sao hirsuta* Barrande. The glabella of *C. walcotti* is outlined by shallow axial furrows that merge along the anterior and posterior margins with a shallow marginal furrow outlining the border. The axial furrows are best developed near the anterior and posterior ends of the glabella. No segmental divisions of the glabella and cheeks are apparent, even under extreme oblique lighting. There is, however, a low, poorly defined elevation at the posterior end of the glabella at the junction of the dorsal and marginal furrows that may represent the approximate position of the posterior margin of the occipital ring.

In ventral aspect (text-fig. 4A; pl. 26, figs. 5,9), a continuous doublure is present only along the posterior two-thirds of the lateral margin and along the posterior margin. The doublure along the anterior margin was apparently divided into three subequal parts separated from the shield by a marginal suture homologous with the combined adult facial and rostral sutures and from each other by sutures homologous with the connective sutures of the adult. The two lateral portions represent the larval free cheeks and the median portion is the larval rostrum.

The hypostome is subquadrate in outline, with short anterior wings and a moderately well defined, posteriorly tapering middle body. Eight short, broad spines are present along the posterior margin.

Stage II (*Metaprotaspid*): (text-fig. 7; pl. 26 figs. 2,6,10). This stage is represented by 61 individuals with axial lengths ranging from 0.45 to 0.65 mm. Seven of the individuals retain a hypostome, and ten retain a hypostome, rostrum, and one or both free cheeks, all slightly displaced.

The carapace, including the free cheeks, is subcircular in outline, moderately arched transversely and longitudinally, and has a truncate posterior margin.

In dorsal aspect (pl. 26, fig. 2), the shield, exclusive of the cheeks, is distinctly narrower from the position of the eyes forward than it is posterior to the eyes. The axis is narrow and poorly defined by shallow axial furrows. A poorly defined occipital ring separates the anterior portion of the glabella from the axial lobe of the protopygidium. No transverse furrows have been observed other than the ones defining the occipital ring. The anterior end of the glabella expands forward and merges with a poorly defined eye ridge that extends posteriorly, adjacent to the facial suture, and includes the undifferentiated palpebral lobe. The axial lobe of the protopygidium extends to the posterior margin of the shield. A poorly defined border is present along the posterior margin adjacent to the axial lobe. The cheeks appear as narrow crescentic strips along the anterolateral margins of the carapace.

In ventral aspect (pl. 26, fig. 6), there is a continuous narrow doublure around the posterior margin between the posterior ends of the palpebral lobes. The doublure around the anterior margin of the carapace is divided by transverse sutures into three parts of subequal length. The median part is the rostrum, and the lateral parts are the doublures of the free cheeks. The hypostome is not significantly different from that of the anaprotaspid.

Stage III (*Early Meraspid*): text-fig. 7, pl. 26, figs. 3,7,11). This stage is represented by over 100 cranidia with axial lengths ranging from 0.50 to 0.75 mm. Five cranidia retain a hypostome. Ten specimens retain a hypostome, rostrum free cheeks and pygidium, and as many as three thoracic segments.

The cranidium (pl. 26, fig. 3) is subtrapezoidal in outline, broadest at the posterior margin, and gently arched transversely and longitudinally. The glabella is narrow, moderately well-defined by the dorsal furrows, and expanded anteriorly. It merges with a poorly defined eye ridge that continues posteriorly, adjacent to the facial suture, and includes the undifferentiated palpebral lobe. The only apparent transglabellar furrow is the occipital furrow. A shallow posterior border furrow is also present.

The free cheeks (pl. 26, figs. 7,11) are simple, narrow, straplike objects. They extend to, but not beyond the posterolateral corners of the cranidium.

The hypostome has a denticulate posterior margin. The denticles, however, are less well defined than in the protaspids and seem to be fewer in number. The poorly defined middle body appears to extend nearly to the posterior margin.

The rostrum is a simple elongate (tr.) plate.

The transitory pygidium (pl. 26, fig. 7) is subquadrate in outline, about two-thirds the size of the cephalon, and bears a median indentation along the posterior margin. The axial lobe is poorly defined by the axial furrows and may show one to three poorly defined rings. It tapers nearly to a point posteriorly and reaches to the posterior margin.

Stage IV: Middle Meraspid: (text-fig. 7, pl. 26, figs. 4,8,12,16). This stage is represented by 64 cranidia with cephalic lengths ranging from 0.75 to 1.00 mm. One cephalon retains a hypostome, rostrum, and free cheeks, and one complete specimen with seven thoracic segments is known.

The cephalon at this stage is subsemicircular in outline, moderately arched longitudinally and strongly arched transversely, with a nearly straight posterior margin and short genal spines. The cranidium (pl. 26, fig. 4) is subtrapezoidal in outline, broadest opposite the occipital furrow. The glabella is parallel sided for most of its length, slightly expanded anteriorly, and reaches to the inner margin of a well-defined border. A shallow palpebral furrow outlines the posterior end of the palpebral lobe which otherwise merges with the fixed cheek. Eye ridges are not apparent. Shallow posterior border furrows are present on the posterior

limbs and a shallow occipital furrow is the only apparent transglabellar furrow.

The free cheeks (pl. 26, figs. 8,12) are simple, with short, blunt genal spines and no distinct separation of the border from the ocular platform.

The hypostome in exterior aspect has prominent anterior wings and an evenly rounded non-denticulate posterior margin. No border is apparent. In interior aspect, short posterior wing processes extend upward from the lateral margins slightly posterior to the midlength of the hypostome.

The rostrum is a simple elongate (tr.) plate as in earlier stages.

The thorax is composed of seven segments in the only complete specimen in the collection. However, the greatest number of segments observed on a specimen from stage III is three, and the smallest number on a specimen from stage V is 10, so there is a possible range of from 3 to 10 thoracic segments for specimens of stage IV. Individual thoracic segments have the same form as those of the adult.

The form of the transitory pygidium (pl. 26, fig. 16) is not significantly changed from that of stage III but it is only about one-third instead of two-thirds the size of the cephalon.

Stage V (Late Meraspid and Holaspid): (text-fig. 7, pl. 25, figs. 1–4,7–25; pl. 26, figs. 13–15,17–24). This stage is represented by several hundred cranidia ranging in axial length from 1.0 to almost 5 mm. Cranidia under 2.0 mm. in axial length belong to meraspid individuals having 10 to 14 thoracic segments. Three meraspid individuals, one of which is enrolled (pl. 26, figs. 13–15), have 10 thoracic segments, and one specimen with 14 thoracic segments is present. Two meraspid cranidia retain a hypostome, rostrum and several attached thoracic segments and one of these also has attached free cheeks. No complete holaspid individuals are present. A holaspid cephalon has been reconstructed from appropriate free cheeks and a cranidium (pl. 25, figs. 4,7,8); and a thorax lacking an associated cephalon but believed to be from an adult, has 15 segments and an attached pygidium (pl. 25, figs. 19,23).

The late meraspid and holaspid specimens are essentially identical except for the number of thoracic segments and a tendency for the smallest late meraspids to have a somewhat more parallel-sided glabella than larger specimens, where the glabella tapers forward.

Specimens in stage V are characterized by the presence of a brim and border on the cranidium; and by a broad, shallow median trough connecting the glabella to a median posterior indentation of the marginal furrow. The rostrum has a corresponding short median posterior projection. The facial suture is opisthoparian. The free cheeks are similar to those of stage IV but have relatively longer genal spines. The hypostome is elongate subquadrate in outline with a rounded posterior margin. The pygidium is subovate in outline with its greatest width about twice its length. The posterior margin arches upward on the axial line so that it resembles an inverted "V" when viewed from the rear. The width of the axial lobe is slightly less than one-third the greatest width of the pygidium, and it extends nearly to the posterior margin. The pygidial doublure is broadest at the anterolateral margin, tapers posteriorly, and is absent behind the axial lobe.

Discussion.—The general features of the development of *C. walcotti* are like those described for other Cambrian trilobites. The developmental stages recognized here can be recognized in the ontogeny of *Strenuella gripi* (Kautsky, 1943) from the Lower Cambrian, *Sao hirsuta* Barrande (Ružiča, 1943) from the Middle Cambrian, and *Olenus gibbosus* (Strand, 1927), *Olenus transversus* (Kaufmann, 1933) and *Welleraspis swartzi* (Rasetti, 1954) from the Upper Cambrian. States II to V are particularly well shown by Rasetti (op. cit., pl. 62, figs. 2,6,8, 9 respectively).

The principal significant new information obtained from this study of the ontogenetic development of *C. walcotti* has to do with the ventral morphology of the cephalon during growth, and the development of the facial suture. Anaprotaspids with preserved free cheeks, rostrum, and hypostomes supply proof for the inference of Ross (1951) that these structures are present in the larval trilobite. The proparian course of the

facial suture in the protaspid period in contrast to the opisthoparian course in the adult, is further evidence for the artificial nature of the Proparia and Opisthoparia as major subdivisions of the Trilobita.

Until more is known of the earliest developmental stages of trilobites, the significance of detailed characteristics of the protaspids of *C. walcotti* cannot be evaluated. At present, there are no described protaspids whose detailed characteristics are comparable to those described here.

INSTARS

An unsuccessful attempt was made to determine the number of instars in the development of *C. walcotti* using the methods tried with apparent success on the associated olenellids (Palmer, 1957). The negative results of the investigation seem to have been due principally to the variation in size within each instar being greater than the average increase in size between instars. Specimens with the same glabellar length, the cephalic dimension that seems to maintain the most constant relation to growth, were identifiable morphologically as belonging to stages III and IV, and IV and V.

SUMMARY

Morphology.—*C. walcotti* is a small trilobite (adult length 15 mm. or less) with a relatively large cephalon bearing genal spines and occupying almost half of the dorsal area of the carapace. As a result of its thick exoskeleton, furrows are subdued on the external surface and well marked on internal molds.

The rostrum is a long (tr.) quadrangular plate extending nearly the full breadth of the anterior portion of the cranidium.

The hypostome is small relative to the adult cranidium and there is no evidence in the adult that it was in contact with either the rostrum or the under side of the cranidium.

The thorax is composed of at least 15 segments and tapers posteriorly to a small

TABLE 1—SUMMARY OF THE ONTOGENETIC DEVELOPMENT OF CEPHALIC CHARACTERISTICS OF *Crassifimbra walcotti* (RESSER)

	Stage I (anaprotaspid)	Stage II (metaprotaspid)	Stage III (early meraspid)	Stage IV (middle meraspid)	Stage V (late meraspid and holaspid)
Glabella	Expanded anteriorly, unfurrowed, extends nearly full length of shield, merges with continuous anaprotaspid border	Expanded anteriorly, unfurrowed, extends to front of shield, merges with ocular ridges	Same	Slightly expanded anteriorly, unfurrowed, reaches to inner edge of border	Parallel-sided to tapered anteriorly unfurrowed except in largest specimens (three pairs of furrows). Separated from border by narrow brim
Eye ridge	Part of anaprotaspid border	Continuous from posterior end of eyes to merger with anterior end of glabella	Same	Not apparent	Apparent as low thin ridge only in largest specimens
Frontal area	Absent	Absent	Absent	Composed of border only	Composed of brim and border
Free cheek	Marginal, dominated by doublure; at anterolateral margins of anaprotaspid shield	Narrow dorsal extension; anterior to widest part of shield	Along entire lateral margin, narrow, no genal spine	Along entire lateral margin, genal spine present	Same
Rostrum	Simple, narrow (Sag.) relatively long (tr.) slightly curved plate	Same	Same	Same	Same, extends across nearly entire anterior breadth of cranidium
Hypostome	Dominated by subtriangular middle body; posterior margin with fringe of eight short spines, anterior margin straight	Same	Same, spines less distinct	Subquadrate in outline with evenly rounded posterior margin; weak anterior wing processes; anterior margin straight	Elongate subquadrate in outline with evenly rounded posterior margin and strong anterior wing processes, anterior margin sinuous
Facial suture	Marginal, proparian	On dorsal surface, proparian	Gonatoparian	Opisthoparian	Opisthoparian

rather featureless pygidium. Position in the thorax of individual thoracic segments can be determined by examining the length (sag.) of the articulating half ring; length (tr.) of the portion of each pleuron distal to the geniculation compared to the length (tr.) of the proximal portion of the pleuron; amount of posterior deflection of the distal portion of each pleuron; and degree of development of the short terminal spine.

The pygidium has a broad axial lobe reaching nearly to the posterior margin, and a narrow doublure present only along the lateral margins.

Open sutures separate the rostrum and cheeks from each other and from the cranidium. In the adult, the sutures separating the free cheeks from the cranidium and the rostrum (facial and connective sutures respectively) are continuous and at a distinct angle to the rostral suture. In the earliest protaspid the facial and rostral sutures are continuous, however, and the connective sutures join them at a distinct angle.

Statistical observations show that at any one locality, form of the cranidium is reasonably constant, indicating little biologic variability. Comparison of supposedly contemporaneous material from different localities 4 or more miles apart indicates small but significant proportional differences in form of the cranidium that are interpreted here as possibly reflecting geographic variation within the species.

Ontogeny.—Five developmental stages can be recognized in the ontogeny of *C. walcotti*. They are summarized below in Table 1.

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GRAYSONITES, A CRETACEOUS AMMONITE IN TEXAS*

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ABSTRACT—Four species of the Cretaceous ammonite genus *Graysonites* Adkins, *nomen nudum*, 1933, are described and the genus is validated. *Graysonites*, belonging to the family Acanthoceratidae, subfamily Mantelliceratinae, is known only from the upper part of the Washita group of Texas; it is Lower Cenomanian. The four new species are *Graysonites lozoi*, *G. fountaini*, *G. adkinsi*, and *G. wooldridgei*.

INTRODUCTION

AMONG the *nomina nuda* of Adkins are *Amblydiscus* Adkins (1933a) and *Graysonites* Adkins (1933b, p. 363,364). *Amblydiscus* Adkins, 1933, *nomen nudum*, has been named *Spathites* by Kummel & Decker (1954), and the genus proposed by Adkins must remain an invalid *nomen nudum*. The group of "*Hoplitoides mirabilis*" Böse (1920, p. 256,257, Pl. 19), non Pervinquiere, which Adkins (1933a) also considered a new genus should now be referred to *Bauchioceras* Reyment (1955), and the forms collected by Adkins have recently received the name *Bauchioceras adkinsi* (Kummel & Decker, 1954). *Graysonites* is still a *nomen nudum* after 25 years. Described below are four species of *Graysonites*, n. gen. *Graysonites lozoi*, n. sp., and *G. fountaini*, n. sp., are manuscript and label names used by Adkins, and it was his desire that *G. lozoi* be the type species of the genus. The holotype of *G. lozoi* is also of his designation.

In so far as known *Graysonites*, n. gen., is restricted to the Del Rio clay, the Grayson marl, the top of the Georgetown limestone, and the top of the Main Street limestone. *G. fountaini*, n. sp., *G. adkinsi*, n. sp., and *G. wooldridgei*, n. sp., are known from the top of the Georgetown limestone and the top of the Main Street limestone. All three of these species are also known from the lower part of the Del Rio clay or the lower part of the Grayson marl. *G. lozoi*, n. sp., is known only from the Del Rio clay and the Grayson marl, and is from a younger zone than the other species.

The ammonite zonation in Texas can now be added to. The zone of *Graysonites adkinsi* n. sp. (=zone of *Graysonites* of Adkins, 1933b, p. 363 and Adkins & Lozo, 1951, p. 154) overlies the zone of *Plesioturrilites brazoense* (Roemer) and the zone of *G. lozoi*, n. sp., overlies the zone of *G. adkinsi*. The exact relationships of the zone of *G. lozoi* with the zone of *Plesioturrilites bosquense* and "*Submantelliceras*" *wacoense* (Adkins, 1933b, p. 363) has yet to be determined, but they are probably in part mutually inclusive.

Graysonites adkinsi is now the proper name for *Acanthoceras* sp. aff. *A. cunningtoni* Böse (Böse, 1928; Adkins, 1933b), non Sharpe. This is one of the species which Böse (1928) used to prove the Cenomanian age of the upper part of the Georgetown limestone. Its misidentification does not alter the age of the Georgetown limestone because Böse (1928) was just as definite that *Plesioturrilites brazoense* (Roemer) proved the Cenomanian age of this formation, as would various species of "*Submantelliceras*" in the upper part of the formation.

I wish to thank Mary Grace Muse Adkins for the opportunity to study fossils from the Adkins Collection, and John T. Lonsdale, Director, Bureau of Economic Geology, The University of Texas, for making Bureau of Economic Geology collections available.

SYSTEMATIC DESCRIPTIONS

Phylum MOLLUSCA
Class CEPHALOPODA
Order AMMONOIDEA
Suborder AMMONITINA Hyatt, 1889
Superfamily ACANTHOCERATACEAE Hyatt, 1900
Family ACANTHOCERATIDAE Hyatt, 1900
Subfamily MANTELLICERATINAE Hyatt, 1903

Genus GRAYSONITES, n. gen.

Type species.—*Graysonites lozoi*, *n. sp.*, from the Del Rio clay, 2 miles southeast of

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Del Rio, Val Verde County, Texas; Lower Cenomanian; deposited in the Adkins Collection.

Generic characters.—Oligogyral, subangustumbilicate, subgradumbilicate; whorl section high, submantellicerine; costation and nodosity submantellicerine in neanic state, ribbing becoming coarse in ephebic stage; hypernodosity dominant in the adults, producing ventro-lateral horns in most species.

Observations.—Arkell, Kummel, & Wright (1957) place *Submantelliceras* Spath in synonymy with *Mantelliceras* Hyatt, 1903, because "*Submantelliceras* includes merely inner whorls of compressed species of this [*Mantelliceras*] and other genera." *Graysonites*, n. gen., is one of these other genera. "*Submantelliceras*" *worthense* (Adkins, 1920) "*S.*" *brazoense* (Böse, 1928) and "*S.*" *wacoense* (Böse, 1928) are all pyritic juveniles of unknown adult affinities. None of these three species compares easily with the juveniles of *Graysonites lozoi*, n. sp., the only one of the four species of *Graysonites* described in this paper of which the juvenile stage is known sufficiently early to compare with the species of "*Submantelliceras*" from Texas. Böse (1928) misidentified *Graysonites*, probably *G. adkinsi*, n. sp., with *Euomphaloceras* aff. *euomphalus* (Sharpe) [*e.g.*, *Acanthoceras* sp. aff. *A. cunningtoni* (Sharpe) in Böse, 1928, p. 152, 153, 160, 161, 166]. How I (Young, 1957) altered this reference to Scott (1926) will never be known.

Acanthoceras athabascense Warren & Stelck does not seem to be an *Acanthoceras*, but its suture is not comparable to that of *Graysonites*, n. gen. The horns of such species of *Mammites* as *M. chivensis* Archanguelsky (1916, pl. 8, figs. 1,5–7) are reminiscent of *Graysonites lozoi*, n. sp., and forms with similar horns also occur in concretions with *Borissjakoceras* sp. in the Frontier formation, at the base of the first thick bentonite bed (10 feet or more thick) below the *Vascoceras* zone on the Little Bighorn River, south-central Montana. Although reminiscent of *Graysonites*, these forms should not be confused with *Graysonites*.

Species such as *Graysonites wooldridgei*, n. sp., could probably be reasonably placed in a group of compressed, tabulate, slightly horned *Mantelliceras*; but the development of species like *G. wooldridgei* into horned forms like *G. lozoi*, together with their unusual suture pattern, the first lateral lobe of which is reminiscent of that of *Neopulchellia* Collignon (1929), seems to warrant their separate generic assignment to *Graysonites*. The suture is quite distinct, even from that of *Neopulchellia*, in the long, narrow siphonal saddle and few elements dorsad of the first lateral lobe.

GRAYSONITES LOZOI Young, n. sp.
Pl. 1, figs. 1–11; Text-figs. 1b,c,d,f

Holotype.—The adult individual illustrated on pl. 1, figs. 3,4, and 8, from the upper Del Rio clay, Val Verde County. The small individual illustrated, in pl. 1, figs. 1,2,6,7,9, and 10 was found inside the larger individual and is almost certainly part of a juvenile whorl. Collectors: W. S. Adkins and F. E. Lozo, November, 1948. In the Adkins Collection, Austin, Texas.

Specific characters.—Oligogyral, slightly excentrumbilicate, subangustumbilicate, subgradumbilicate; the whorl section high throughout, the height/width ratio ranging from 1.41 upward; the measurements on the holotype are not to be trusted because the individual is crushed an undetermined amount. Overlap is to about mid-flank; whorl section is tabulate to subtabulate ventrally, being more tabulate in the younger whorls, the large horns modifying the shape of the venter at greater diameters.

An inner fragment representing an individual about 45 mm. in diameter is submantellicerine and appears much like *Neopulchellia gignouxi* Collignon (1928, pl. 18, figs. 18,18ab only), but the ribbing and nodosity is stronger on *G. lozoi*. At this diameter the umbilical nodes are bullate, the ventrolateral nodes slightly bullate, and the peripheral nodes high and clavate. The suture is mantellicerine at the 45 mm. diameter, but already phylloid elements are appearing in the saddles. The transition from the inner whorls to the *Graysonites* hypernodosity is missing, but by a diameter of 110 mm. the ventrolateral horn is 12 mm. long, the peripheral clavae have disappeared and each umbilical bulla has divided into two bullae on a raised rib, one bulla radial to the other. With increasing diameter the ventrolateral horns keep increasing in size

until they reach a length of 30 mm. or more. The large specimen (pl. 1, figs. 5,11) is the last whorl of an adult individual; on the last half of the body chamber the horns decrease in size, the umbilical bullae decrease in size, and the peripheral clavae reappear, resulting, near the aperture, at a diameter of 215 mm., in a whorl section again strikingly submantellicerine. Fragments of other ammonites, twice the size of the largest individual of *G. lozoi*, n. sp., are known from the Del Rio clay; these apparently never lose their submantellicerine whorl section and costation at any stage of growth and represent a different genus.

Rib density at a 45 mm. diameter is about 32 ribs per volution, about $\frac{1}{3}$ of which are primary with umbilical bullae and $\frac{2}{3}$ of which are intercalating; at this diameter the costae and intercostae are about equal in width. At a diameter of 155 mm. rib density is about 14 ribs per volution, all primary, and the intercostae are about 3 times the width of the costae. This density continues to greater diameters.

The holotype is septate throughout and the maximum diameter is about 155 mm. The larger individual reaches a diameter of 215 mm., the aperture being present, but so poorly preserved as to defy description. On this larger individual the last septum occurs at about 155 mm., and the body chamber occupies approximately 180° of the last volution.

The suture is quite distinct, with deep ventral lobe, long first lateral lobe, and much shorter elements dorsad of the first lateral lobe. The saddles, even to the 2nd and 3rd grade, are distinctly phylloid.

Measurements of two individuals are as follows, the letter symbols being those of Young (1957):

	D	U	H	W	H/W
holotype	155.0	27.0	40.0	21.0	1.92
	120.0	21.0	41.0	21.0	1.96
	42.5	21.0	47.0	26.0	1.82
	30.0	—	50.0	30.0	1.66
paratype	215.0	31.0	39.5	25.5	1.52
	175.0	33.0	40.0	26.0	1.52
	145.0	—	41.5	29.5	1.41

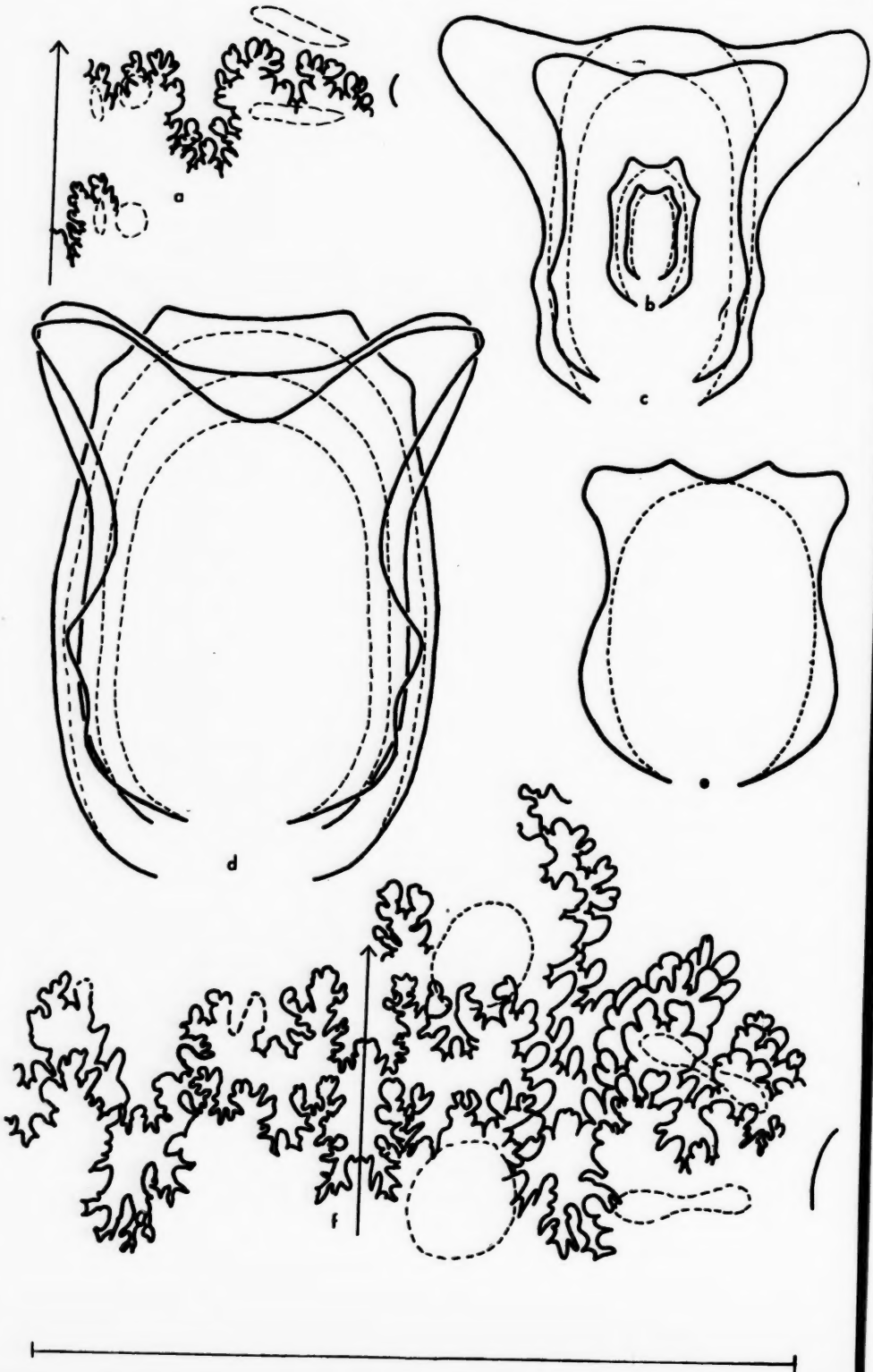
Observations.—Graysonites lozoi, n. sp., is the most ornate of the known species of *Graysonites*. It develops adult features earlier and has longer horns than the other species. *G. lozoi* is also distinct from other species, in the adult, in the development of two small bullae from each umbilical bulla. In other species the umbilical bullae remain single. In *G. lozoi* these double bullae are arranged radially, one ventrad of the other.

The question still remains as to the relashiip of *G. lozoi*, n. sp., to "*Submantelliceras*" *wacoense* Böse and "*S.*" *brazoense* Böse. "*S.*" *aumalense* (Coquand), "*S.*" *suzannae* (Pervinquiere), "*S.*" *martimpreyi* (Coquand) and "*S.*" *worthense* (Adkins) have flat flanks, with nodosity decreasing or absent on the second and third fifths of the flank. Costation remains pronounced on all of the flank of the youngest stage known in *G. lozoi;* however, this stage is slightly larger than that of "*S.*" *suzannae*, and perhaps larger than some of the others. At equivalent diameters "*S.*" *wacoense* Böse and "*S.*" *brazoense* Böse seem to have slightly more pronounced nodosity than *G. lozoi* although the ribs are of about the same size and density. The forward inclination of the ribs from the ventrolateral node to the ventral clava seems to be less on *G. lozoi* than on Böse's two species of "*Submantelliceras.*"

The odds seem to favor that Böse's two species of "*Submantelliceras*" are pyritized juveniles of some species of *Graysonites*, but a specific assignment to an adult form is not yet possible. "*S.*" *worthense* (Adkins) is probably not a *Graysonites*, but only because no known *Graysonites* of any size have been found in beds that correlate with the strata in which "*S.*" *worthense* occurs.

In the zone of *G. lozoi* also occur species similar to "*S.*" *suzannae* (Pervinquiere) and "*S.*" *aumalense* (Coquand) with weak ribs or no ribs on the first one-half of the flank. These are not the forms identified by Scott (1926) with "*S.*" *suzannae* and "*S.*" *aumalense;* Scott's forms were from lower in the section (Pawpaw instead of Grayson) and have been identified by Adkins (1928) with his "*S.*" *worthense*. Adkins's species is still of unknown adult affinities.

K559 (pl. 2, figs. 5,6; text-figs. 1a,2d) may be another fragmental individual of *G. lozoi*, representing a different diameter. The suture is not as phylloid as in the holotype, and the horns are directed laterad rather than ventrolaterad; the individual does have


a
b
c
d
f

radially arranged double bullae developed from the single umbilical bulla of the submantellicerine stage.

Localities and horizons.—Only two individuals of *G. lozoi*, n. sp., are known. The holotype is from the top of the Del Rio clay, 2 miles southsoutheast of Del Rio, from a road cut on the El Indio road, Val Verde County, Texas. The paratype is from the Grayson formation (position undetermined), Zion Creek, Cooke County; Lower Cenomanian; both individuals are in the W. S. Adkins Collection.

GRAYSONITES WOOLDRIDGEI Young, n. sp.
Pl. 2, figs. 1–4; pl. 3, figs. 2,4; text-figs. 3c,d,f

Holotype.—UT 19819, from the Grayson formation, in limy beds near the base, ¼ mile above the old ford across Big Elm Creek on the Denton-Pilot Point road, Grayson County. Coll.: Jasper Wooldridge, 25 July, 1892.

Specific characters.—Oligogyral, concentrumbilicate, subangustumbilicate, subgradumbilicate; the whorl section is high and narrow throughout, height/width ratio varying from 1.42 to 1.68. Overlap is to about mid flank; intercostal section is tabulate to subtabulate ventrally. The costal section shows considerable variation during the ontogeny, but up to 90 mm. diameter it roughly parallels the intercostal section except for the nodes. Nodosity up to 90 mm. diameter consists of umbilical bullae, greatly elongated ventral clavae, and ventrolateral nodes. The nodes and ribs up to this diameter (90 mm.) are typically submantellicerine. Beyond 90 mm. the ventrolateral nodes begin gradually to develop into small horns, which, as they become larger, tend to submerge the ventral clavae until they are very faint. The ribs are low, and beyond the 90 mm. diameter the umbilical bullae begin to enlarge until they make up all that remains of the rib; a small area covering about the third ¼ of the flank bearing no ribs or nodes, or only extremely faint, low ribs. Ribs are dense to about 85 mm., at which diameter they become less dense, as the horns and umbilical bullae increase in size. The first half of the whorl ending at a diameter of 125 mm. has about 20 ribs, and the intercostae and costae are about the same width. The last half of the same whorl has only about 12 ribs, and on the last ¼ of the whorl, which is part of the body chamber, the intercostae are about 2½ times the width of the costae. Rib density at 100 mm. would seem to range from 26 to 34 ribs per volution, some individuals starting to develop hypernodosity and coarse costation at earlier shell diameters than others.

The holotype, UT 19819, is the only individual retaining any of the body chamber; it is septate to a diameter of 116 mm. The fossils are all internal molds, so that no information is available concerning apertural features.

It was not possible to recover a suture from the holotype, but an individual in the Adkins Collection (pl. 3, figs. 2,4; text-fig. 3f) shows the suture reasonably well, although the individual is eroded. The wide first lateral saddle is shown; the suture is more mantellicerine than is that of the type species, *G. lozoi*, n. sp. (text-fig. 1f), the ventral lobe in *G. wooldridgei* not being as deep, and the first lateral lobe not being as long.

The following measurements are representative of the small number of individuals of this species available for study.

EXPLANATION OF TEXT-FIG. *1*

a—*Graysonites* sp. Suture, ×1; see also pl. 2, figs. 5,6, and text-fig. 2d; K559, W. S. Adkins Collection.
b—*Graysonites lozoi* Young, n. sp. Whorl sections at diameters of 30 and 42.5 mm. of the small fragment found in place inside of larger fragment (c of this figure); see also pl. 1, figs. 1,2,6,7,9,10.
c,f—*Graysonites lozoi* Young, n. sp., *c*, whorl sections of holotype at diameters of 120 and 155 mm.; see also pl. 1, figs. 3,4,8; *f*, suture of same individual; both ×1.
d—*Graysonites lozoi* Young, n. sp. Whorl sections at diameters of 145, 175, and 215 mm. ×1; see also pl. 1, figs. 5,11.
e—*Graysonites adkinsi* Young, n. sp. Whorl section of holotype at a diameter of 115 mm.; UT 272, ×1; see also pl. 3, figs. 1,7.

	D	U	H	W	H/W	P	S	B	T
UT 19808	110.0	27.5	43.5	28.0	1.54				
UT 19819 holotype	125.0	26.5	45.0	26.5	1.66	16	16	—	32
	100.0	25.5	47.5	30.0	1.58				
	75.0	21.5	46.5	28.0	1.67				
	60.0	21.0	45.0	28.5	1.59				
Adkins Coll.	107.0	26.0	44.0	31.0	1.42				
	72.0	32.0	44.5	26.5	1.68				

Rib counts on UT 19808, ½ volution, and the individual from the Adkins Collection, also ½ volution, would be misleading because these individuals represent the stage of rapid decrease in the density of costation.

Observations.—It is difficult to compare any of the species of *Graysonites* with the "submantellicerines" of Texas because all of the latter are "micromorphs" (*e.g.*, not dwarfs, but pyritized juveniles in the Texas forms). Since *Graysonites wooldridgei*, n. sp., occurs in the zone of *G. adkinsi*, n. sp., which overlies the zone of *Plesioturrilites brazoense* (Roemer), it must be younger than "*Submantelliceras*" *worthense* (Adkins) because the latter (Young, ms.) can be no younger than the lower and middle parts of the zone of *Plesioturrilites brazoense*. This, of course, does not prove that the two are different species, and furthermore, *G. wooldridgei* is not known in an ontogenetic stage comparable to that of "*Submantelliceras*" *worthense*. The latter probably does not belong to *G. wooldridgei*, and probably does not even represent a species of *Graysonites*, since undoubted species of *Graysonites* have not been found below the top of the zone of *Plesioturrilites brazoense*.

A like approach can be made with "*Submantelliceras*" *wacoense* Böse and "*S.*" *brazoense* Böse. These two fossils occur in what at this time is best termed the zone of *Graysonites lozoi*, n. sp., or the zone of *Plesioturrilites bosquense* (Adkins), since *G. lozoi* is so rare as to result in a rather ill-defined zone. At least Böse's two species are younger than any undoubted *G. wooldridgei*. Also the nodosity on "*S.*" *wacoense* and "*S.*" *brazoense* is coarser than is to be expected on a comparable stage in *G. wooldridgei*.

Graysonites wooldridgei, n. sp., is easily distinguished from the other three species of the genus, *G. lozoi*, n. sp., *G. adkinsi*, and *G. fountaini*, n. sp., because *G. wooldridgei* maintains the mantellicerine type ribbing to a greater diameter (*e.g.*, to 90 or 100 mm. diameter) whereas the other species begin to illustrate the *Graysonites* hypernodosity at much earlier diameters.

Horizon and localities.—*Graysonites wooldridgei*, n. sp., is known only from the zone of *Graysonites adkinsi*, n. sp., Grayson formation of Cooke County, top of the Main Street limestone in Hill County, and top of the Georgetown limestone, Travis County, Texas; Lower Cenomanian.

GRAYSONITES ADKINSI Young, n. sp.

Pl. 3, figs. 1,7; text-figs. 2a,e,f,3a,e

Acanthoceras aff. *cunningtoni* Böse (non Sharpe) 1928, p. 152,153,160,161,166.

Acanthoceras aff. *cunningtoni* Böse in Adkins, 1933b, p. 385–387.

Holotype.—UT 272, from the top of the Main Street limestone, east of highway 81

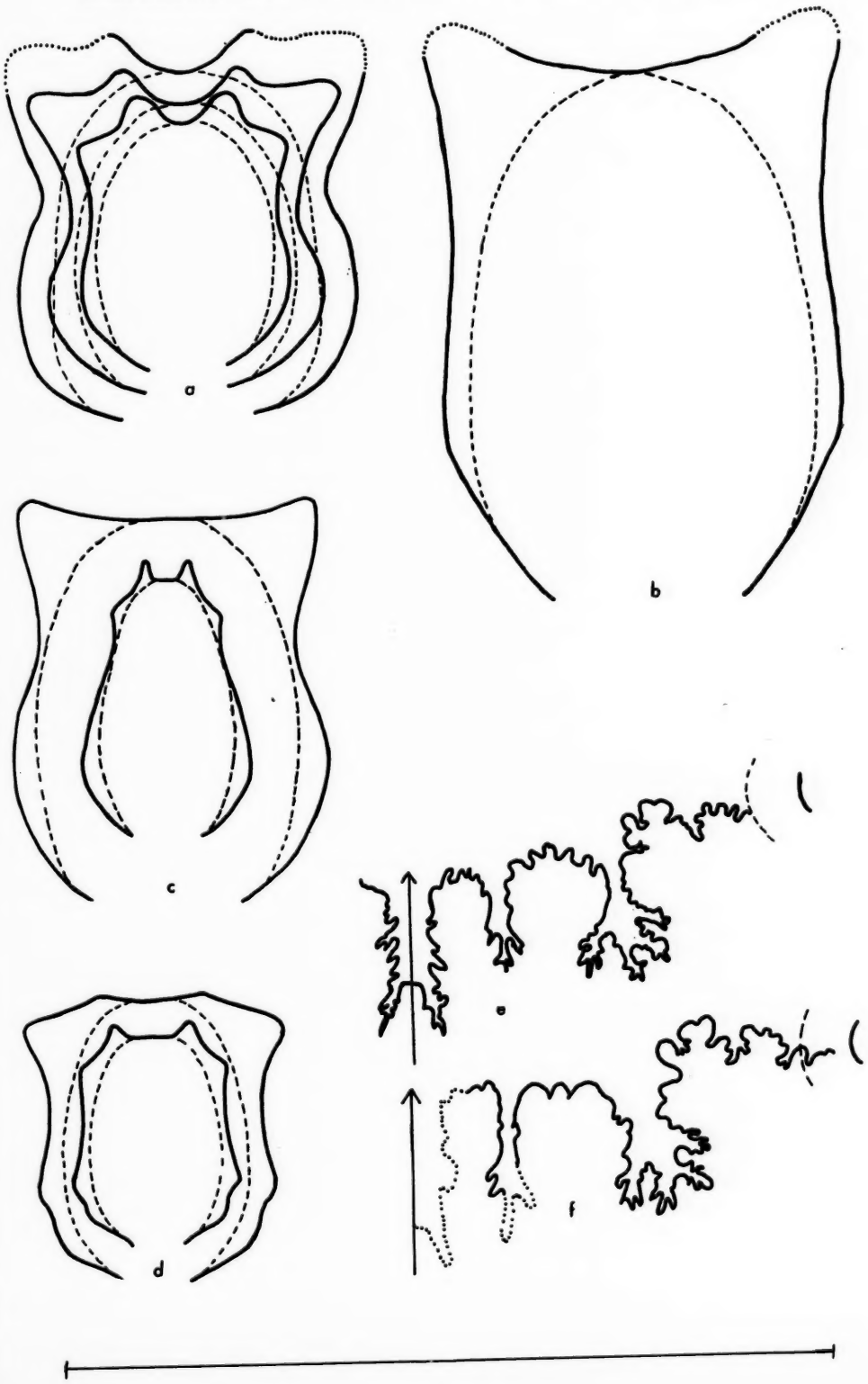
EXPLANATION OF TEXT-FIG. 2

a,e,f—*Graysonites adkinsi* Young, n. sp. *a*, whorl sections at 75, 100, and 125 mm. diameters, ×1; *e,f*, consecutive sutures, *f* at a 100 mm. diameter, *e*, the suture preceding. The variations in the first lateral lobe are to accommodate the slightly different positions of the suture in relation to the position of the large ventrolateral horn; from Bell County, horizon undesignated, but the lithology indicates the Main Street limestone-Del Rio clay transition beds; W. S. Adkins collection. no. 3043a.

b—*Graysonites fountaini* Young, n. sp., (?). Whorl section of a large fragment; see also pl. 3, fig. 5; W. S. Adkins Collection.

c—*Graysonites fountaini* Young, n. sp. Whorl sections of holotype, BEG 19054, ×1, at diameters of about 95 and 140 mm.; see also pl. 3, figs. 3,6.

d—*Graysonites* sp. Whorl sections ×1; see also pl. 2, figs. 5,6, and text-fig. 1a; K559, W. S. Adkins Collection.


a
b
c
d
e
f

(Belton-Georgetown), at the top of the south bluff of the Lampasas River, south of Belton, Bell County. Collector: K. Young, 1950.

Specific characters.—Oligogyral, excentrumbilicate, narrowly subangustumbilicate in juvenile to widely subangustumbilicate in the adult, subgradumbilicate; the whorl section is higher than wide, ranging from 1.23 to 1.6; the figures above 1.45 may be the result of compaction of sediments; overlap is not quite to mid flank in the adults. The intercostal section is tabulate to about 60 mm., then becoming oval and remaining oval to all greater diameters. The submantellicerine stage is not well preserved, and a whorl section at this stage cannot be recovered; beyond the submantellicerine stage the costal section is roughly quadrangular because of the positioning of the nodes. Nodosity beyond the submantellicerine stage consists of strong and long umbilical bullae, ventrolateral nodes, and ventral clavae. The largest individual in the collection reaches a diameter of about 125 mm., and the ventrolateral nodes increase in size gradually until they become horns. The diameter at which nodes change to horns is variable, but 90 mm. plus or minus 15 mm. probably covers the range of variability. The ventral clavae persist strongly to the 125 mm. diameter. Low ribs continue beyond the 90 mm. diameter, but are so low as to be almost inconspicuous between the strong umbilical bullae and the even stronger ventrolateral horns.

Ribs are moderately dense at diameters of 50 mm. or less, the intercostae being about one and one-half times the width of the costae; decreasing in density, there being about 20 ribs per volution at a 75 mm. diameter, 17 ribs at 120 mm. diameter of UT 272, and 15 ribs at the 125 mm. diameter in WSA 3043a. There is some variation in the direction of inclination of the horns; this is probably best illustrated (text-figs. 2a,3a,e).

All individuals are septate throughout and they are all internal molds; consequently no apertural features can be described. Rather ill defined sutures are visible on UT 272 and these agree reasonably well with those of WSA 3043a (Text-figs. 2e,f). The sutures have a long ventral lobe, a wide and little partitioned first lateral saddle, to accommodate the large ventrolateral horn, and a long, narrow first lateral lobe, the width of which varies depending on its relative position to the ventrolateral horn. The auxillary lobe in the first lateral saddle is so positioned as to ride the low space between the ventral clava and the ventrolateral horn. Between the first lateral lobe and the umbilical seam there are 4 or 5 rather poorly defined lobes of little importance.

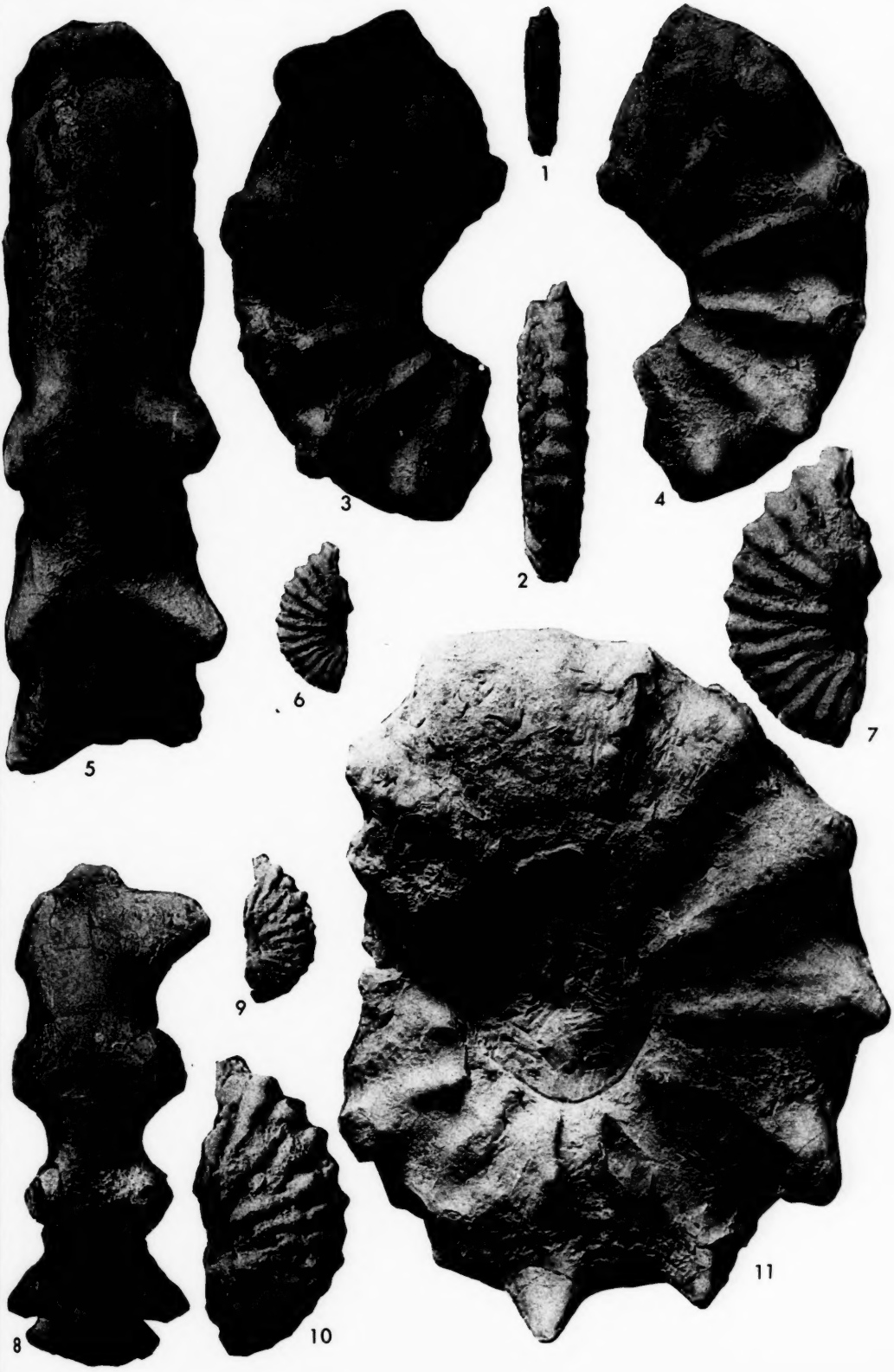
Septal density is one or two septa per volution greater than rib density in the adults. As a result there is a tremendous variation in the suture pattern depending on whether the septum passes just apicad of a horn, just orad of a horn, over a horn, or intermediate between two horns. There is a variation in different elements of the suture depending on their individual proximity to a horn.

In the following measurements some of the figures for UT 272 may be too small by some unknown quantity because this fossil was crushed during compaction of the sediments.

	D	U	H	W	H/W	Ribs
WSA 3043a	125.0	26.0	44.0	35.0	1.25	15 primary
	100.0	29.0	44.5	36.0	1.23	
	75.0	32.0	51.5	38.0	1.35	
UT 272 holotype	120.0	27.5	44.0	27.5	1.60	
	100.0	29.0	45.0	31.0	1.45	
	75.0	—	46.5	30.5	1.52	

EXPLANATION OF PLATE 27

FIGS. *1–11*—*Graysonites lozoi* Young, n. sp. *1,2,6,7,9,10*, ventral and lateral views of the small individual from inside of the large individual shown on this plate in figures 3,4,8 and in Text-fig. 1b. *3,4,8*, lateral and ventral views of holotype (see also text-figs. 1c,f). *5,11*, ventral and lateral views of large individual; see also text-fig. 1d. *1,6,9*, ×1; *3–5,8,11*, ×½; *2,7,10*, ×2; *1–4,6–10*, from the top of the Del Rio clay, 2 miles SE of Del Rio, Val Verde County, Texas; *5,11*, from the Grayson marl, Zion Creek, Cooke County, Texas. All specimens from the W. S. Adkins Collection.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Observations.—Four individuals of *Graysonites adkinsi*, n. sp., are known at this writing. The location of the forms discussed by Böse (1928) is not known; they could not be located in the Bureau of Economic Geology. The designation of *Acanthoceras* aff. *cunningtoni* (Sharpe), the comparison with *Acanthoceras cunningtoni* (Sharpe) var. *cornutum* plus a horizon in the top of the Georgetown limestone, suggest that *G. adkinsi* is the species that Böse (1928, p. 152,153,160, 161,166) had in mind; there is no other species in Texas which has this appearance that is also found in the Georgetown limestone. This is also the species Adkins used (see *Graysonites*, Adkins, 1933b, p. 363, and Adkins & Lozo, 1951, p. 154) for his *Graysonites* zone; it is the only really "horned" species which occurs below the *Plesioturrilites bosquense* zone and above the *Plesioturrilites brazoense* zone. On the other hand, on page 385, Adkins indicates two species in this zone, here called "*Acanthoceras* aff. *cunningtoni* Böse." On page 386 Adkins uses "*Acanthoceras* aff. *cunningtoni* Böse," and also on page 387, where he adds, "a fossil practically restricted to this level [the transitional zone between the Main Street limestone and the Grayson marl]." It seems that in 1933 Adkins was as yet unfamiliar with the younger *Graysonites lozoi*, n. sp., which he later selected to be the type species; furthermore, his use of the generic term on page 385 suggests that Adkins was thoroughly familiar with the subfamily affinities of the genus as also do remarks on some of the labels of fossils in the Adkins Collection.

Graysonites adkinsi, n. sp., attains the *Graysonites* hypernodosity at a much earlier diameter than does *G. wooldridgei* which occurs in the same zone. The development of the horns and the ventral aspect of *G. adkinsi* differentiates it from *G. fountaini*, n. sp., and *G. lozoi* has a more phylloid suture and two radially arranged bullae on and near the umbilicus. Like *G. wooldridgei* and *G. fountaini*, *G. adkinsi* occurs in a horizon well above known "*S.*" *worthense* (Adkins) and below known "*S.*" *brazoense* Böse and "*S.*" *wacoense* Böse. Although this proves nothing it is indicative of differences. No known individuals of *G. adkinsi* have juvenile stages preserved that are small enough to compare with the pyritic juveniles representing the three Texas species of "*Submantelliceras.*"

Horizon and localities.—As Adkins pointed out (1933b, p. 387), *Graysonites adkinsi* is practically restricted to the transition lithology between the Main Street limestone and the Grayson marl. In the north part of Texas this zone is more marly and usually mapped with the Grayson marl. From Hill County southward it becomes progressively more limy and is mapped with the Main Street limestone or the Georgetown limestone. This zone should now be designated the *Graysonites adkinsi* zone and includes the sequence of strata between the top of the zone of *Plesioturrilites brazoense* (Roemer) and some as yet ill-defined upper limit. Above the *G. adkinsi* zone the biostratigraphy of the Grayson marl and biostratigraphical equivalent formations is incompletely worked out, but some place above the *G. adkinsi* zone is the zone of *G. lozoi*. The top of the *G. adkinsi* zone is also marked by the base of the zone of *Plesioturrilites bosquense* (Adkins) (Adkins & Lozo, 1951, p. 154). *G. adkinsi* is known from Hill County, Bell County, Travis County, and Hays County, Texas; Lower Cenomanian.

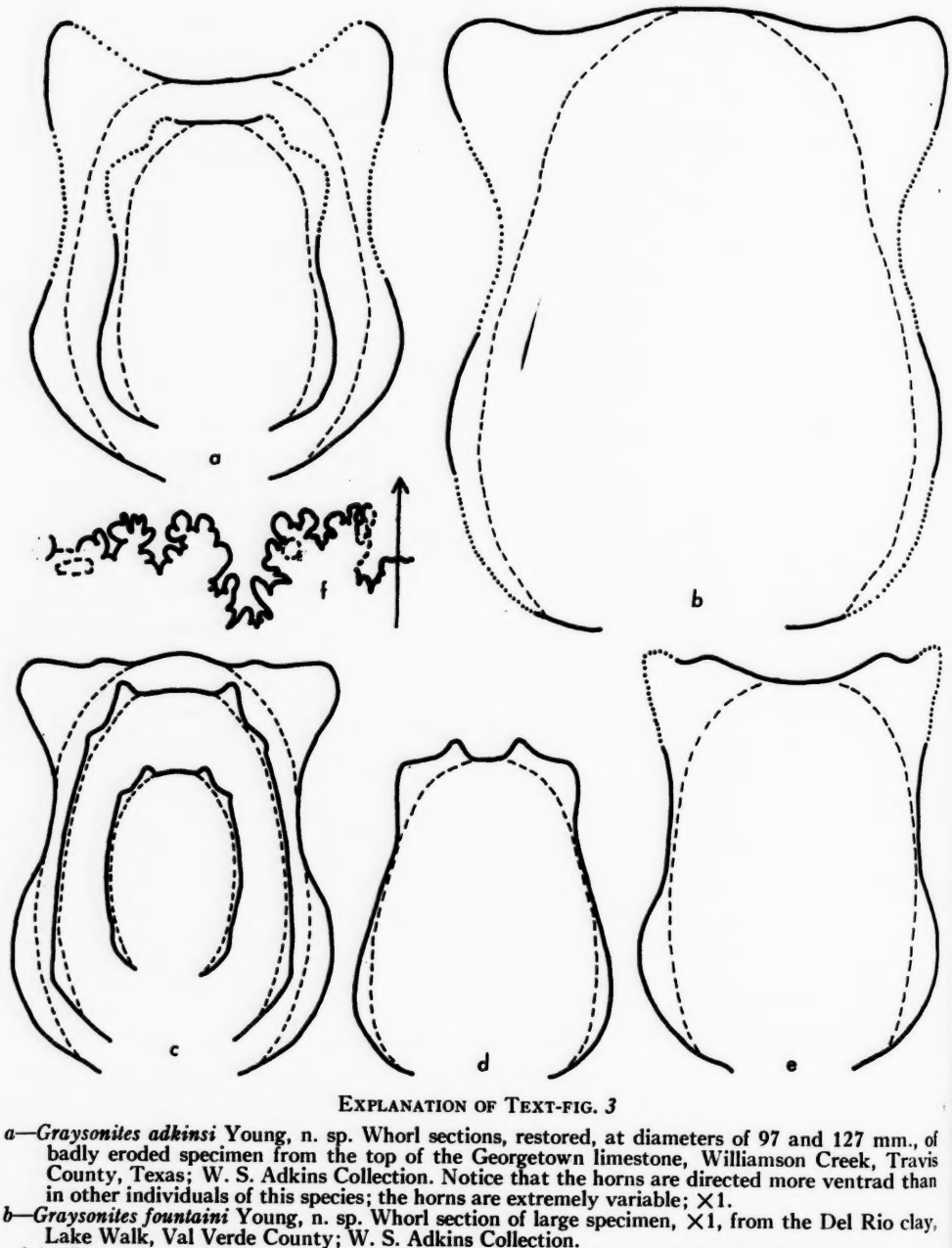
GRAYSONITES FOUNTAINI Young, n. sp.
Pl. 2, figs. 3,6(5?); text-figs. (2b?), 2c,3b.

Holotype.—BEG 19054, from the top of the Main Street limestone (lowest exposed bed), on the South Bosque River about 100

EXPLANATION OF PLATE 28

FIGS. *1–4—Graysonites wooldridgei* Young, n. sp. Ventral and lateral views of holotype, UT 19819, ×1; see also text-fig. 3c; from the Grayson marl, ¼ mile above the old ford on the road from Denton to Pilot Point on Big Elm Creek, Denton County, Texas; collected by Jasper Wooldridge, 25 July, 1892.

5,6—Graysonites, n. sp. Lateral and ventral views of K559, W. S. Adkins Collection, ×1; see also text-figs. 1a, 2d; from the Del Rio clay, on the Kitt Ranch, Kinney County, Texas.



EXPLANATION OF TEXT-FIG. 3

a—*Graysonites adkinsi* Young, n. sp. Whorl sections, restored, at diameters of 97 and 127 mm., of badly eroded specimen from the top of the Georgetown limestone, Williamson Creek, Travis County, Texas; W. S. Adkins Collection. Notice that the horns are directed more ventrad than in other individuals of this species; the horns are extremely variable; ×1.

b—*Graysonites fountaini* Young, n. sp. Whorl section of large specimen, ×1, from the Del Rio clay, Lake Walk, Val Verde County; W. S. Adkins Collection.

c,d,f—*Graysonites wooldridgei* Young, n. sp. *c*, whorl sections of holotype, UT 19819, at diameters of 55, 114, and 125 mm.; see also pl. 2, figs. 1–4; *d*, whorl section of UT 19808, from the top of the Georgetown limestone, Bear Creek, Hays County, Texas; *f*, Suture at a diameter of about 85 mm.; see also pl. 3, figs. 2,4; all ×1.

e—*Graysonites adkinsi* Young, n. sp., (?). Whorl section of ½ volution, ×1; from the top of the Main Street limestone, Tinner Creek, Hill County, Texas; W. S. Adkins Collection.

feet upstream from its junction with the Middle Bosque River, about 6 miles west of Waco, McClennan County, Texas. Collector: W. S. Adkins.

Specific characters.—Oligogyral, concentrumbilicate, moderately subangustumbilicate, subgradumbilicate, whorl section higher than wide, height/width ratio about 1.7 at a diameter of 95 mm., but this may be the result of distortion: height/width ratio about 1.4 on the outer whorl. Overlap is to dorsad of mid-flank on the last whorl; to about mid-flank on earlier whorls. The intercostal section is submantellicerine to about 100 mm., being tabulate or near tabulate on the venter. Although typical submantellicerine costation is lost prior to a 40 mm. diameter, the submantellicerine sections are retained to greater diameters. At 100 mm. diameter there are high ventral clavae, low ventrolateral nodes, and long umbilical bullae, the highest points of which are about 10 mm. ventrad of the umbilical shoulder.

At a 100 mm. diameter there are 14 ribs per one-half volution, 4 of which are intercalating. On the outer whorl there would be about 16 ribs per volution, and on the outer whorl the ventral clavae have been completely suppressed, leaving a tabulate costal section with low ventrolateral horns directed laterad, and long umbilical bullae. At a diameter of 100 mm. the intercostae are about equal in width to the costae and on the outer whorl the intercostae are twice as wide as the costae. The one-fifth volution representing the fragmental outer whorl is body chamber. There is no suture recoverable.

Only a few measurements could be made on the holotype; they are as follows.

D	U	H	W	H/W
95.0	22.0	46.0	26.5	1.73

Observations.—The trivial name of *Graysonites fountaini*, n. sp., is of Adkins's choice, appearing on one of the labels in the Adkins Collection. This species occupies about the same horizon as *G. adkinsi*, n. sp. The inner ends of the ribs on the smallest visible whorl are too well pronounced and too bullate to identify *G. fountaini* with "*Submantelliceras*" *wacoense* Böse or "*S.*" *brazoense* Böse. *G. fountaini* differs from *G. adkinsi* in the suppression of the ventral clavae in later stages, and in the low ventrolateral nodes at comparable stages; hypernodosity does not occur at stages as young as it does in *G. adkinsi*. *G. lozoi* has the double umbilical bullae (radially arranged) not present in *G. fountaini*, and *G. wooldridgei* retains the dense submantellicerine costation to greater diameters.

Horizon and localities.—*Graysonites fountaini*, n. sp., occurs in the zone of *G. adkinsi*. Individuals are known from the Del Rio clay in Val Verde County, the top of the Main Street limestone in McLennan County, and the Del Rio clay in Pecos County.

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MANUSCRIPT RECEIVED JUNE 5, 1957

EXPLANATION OF PLATE 29

FIGS. *1,7—Graysonites adkinsi*, Young, n. sp. Ventral and lateral views of holotype, UT 272, ×1; see also text-fig. 1e; from the top of the Main Street limestone east of highway 81 (Georgetown-Belton), at the top of the south bluff of the Lampasas River, south of Belton, Bell County, Texas; collected by K. Young, 1950.

2,4—Graysonites wooldridgei Young, n. sp. Ventral and lateral views of small specimen, ×1; see also text-fig. 3g; from the top of the Main Street limestone, Tinner Creek, Hill County, Texas; W. S. Adkins Collection.

3,6—Graysonites fountaini Young, n. sp. Ventral and lateral views of holotype, BEG 19054, ×½; see also text-fig. 2c; from the top of the Main Street limestone, 100 feet up the South Bosque River from its junction with the Middle Bosque River, about 6 miles west of Waco, McLennan County, Texas.

5—Graysonites fountaini Young, n. sp., (?). Lateral view of large fragment, ×½, from the Del Rio formation, Lake Walk, Val Verde County; W. S. Adkins Collection.

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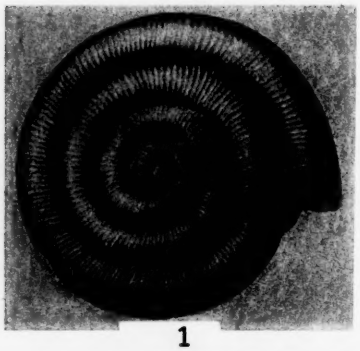

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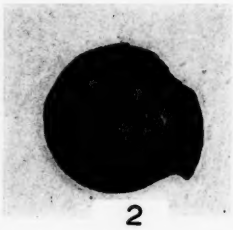

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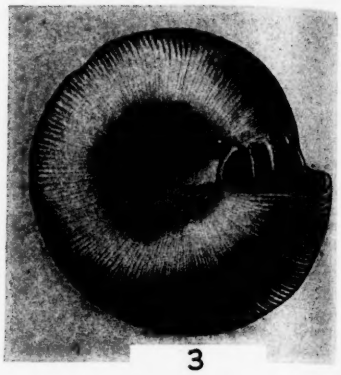

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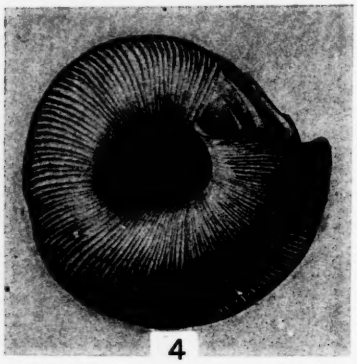

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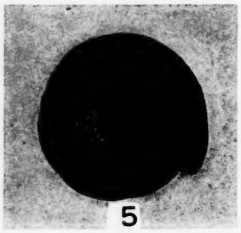

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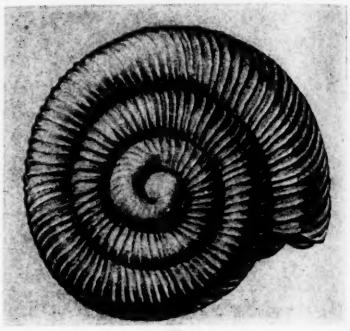

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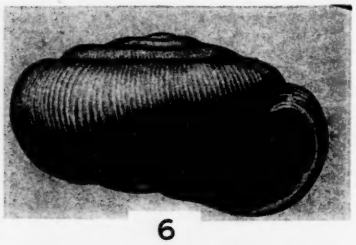

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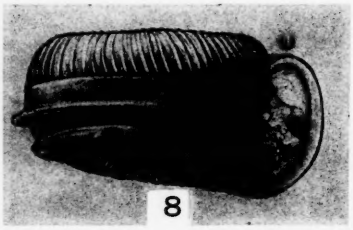

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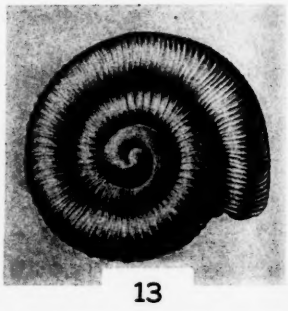

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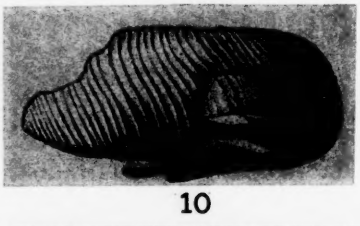

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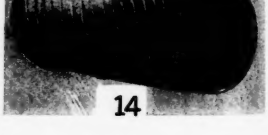

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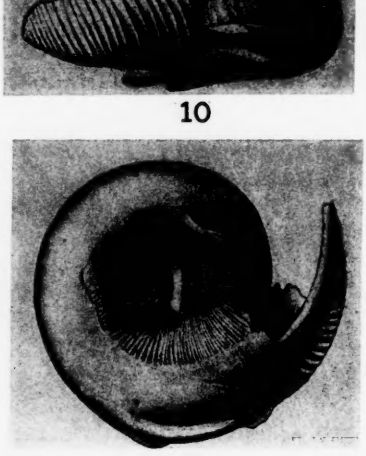

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JOURNAL OF PALEONTOLOGY, V. 32, NO. 1, P. 183–198, PL. 30, 5 TEXT-FIGS., JANUARY 1958

FOSSIL LAND SHELLS FROM WESTERN PACIFIC ATOLLS[1]

HARRY S. LADD
U. S. Geological Survey, Washington, D. C.

ABSTRACT—Shells of 4 species of minute endodont land snails have been recovered from drill holes on Bikini, Eniwetok, and Funafuti Atolls from lagoonal deposits now lying 170 to 1800 feet below sea level. All of the species belong to a group that is widely distributed today in Polynesia and Australasia where, almost without exception, they are found in forested areas on leaf mold or rotting wood or on trees in the forests of high islands. The species here described seem to be the first known fossil representatives.

Shells of 2 Quaternary species (*P. inexpectans* and *P.* sp. A) are well preserved though they occur in lithologic units where corals and most marine mollusks are found chiefly as molds. When these land snails lived, the upper parts of what are now sea level atolls may have been forested islands standing well above the sea. During these emergent stages, many aragonitic shells and skeletons were removed by solution or recrystallized to calcite.

Two Miocene species ((*P. subpacificus* and *P. eniwetokensis*) each represented by a single incomplete shell) exhibit the coloration of the marine fossils with which they are associated. Their occurrence between leached zones suggests that some land projected above the sea during the Miocene when thick lagoonal deposits were accumulated. Dense concentrations of pollen have been obtained from the upper Milocene section drilled on Eniwetok Atoll and these occurrences strongly support the postulated emergence.

The fossil land shells are related to forms living today in other parts of Polynesia and in Melanesia but the meagerness of the fossil record limits speculation on genetic relationships. Several modes of dispersal for such minute forest-loving snails are considered, that by storm winds being favored.

The occurrences bear directly on the subsidence theory for the origin of coral reefs, as they suggest that the overall history of subsidence was interrupted by periods of emergence. In the past, many atolls may have served as high island stepping-stones in the distribution of life in the Pacific.

INTRODUCTION

Samples obtained from a number of deep holes drilled on coral atolls in the Marshall and Ellice Islands contain r ch marine assemblages. In addition to mollusks there are many Foraminifera, corals, and reef-building algae. All occur from the surface downward, the deepest holes penetrating 1,500 feet of Eocene limestone for a total depth of more than 4,000 feet. In sorting fossil mollusks from Bikini drill cuttings from a depth of 450 feet, 7 specimens of a minute land shell were found. The shells represent an undescribed endodont (Family Endodontidae) belonging to the genus *Ptychodon* that is widely distributed today on the high islands of Polynesia and Australasia. Continued searching yielded a single example of a second undescribed species in a sample collected at 166 feet in the deep hole drilled by the British on Funafuti; still later two other specimens were found, one at a depth of more than 1,800 feet on Bikini, the other at a depth of some 800 feet on Eniwetok (Text-fig. 1).

[1] Publication authorized by the Director, U. S. Geological Survey.

EXPLANATION OF PLATE 30

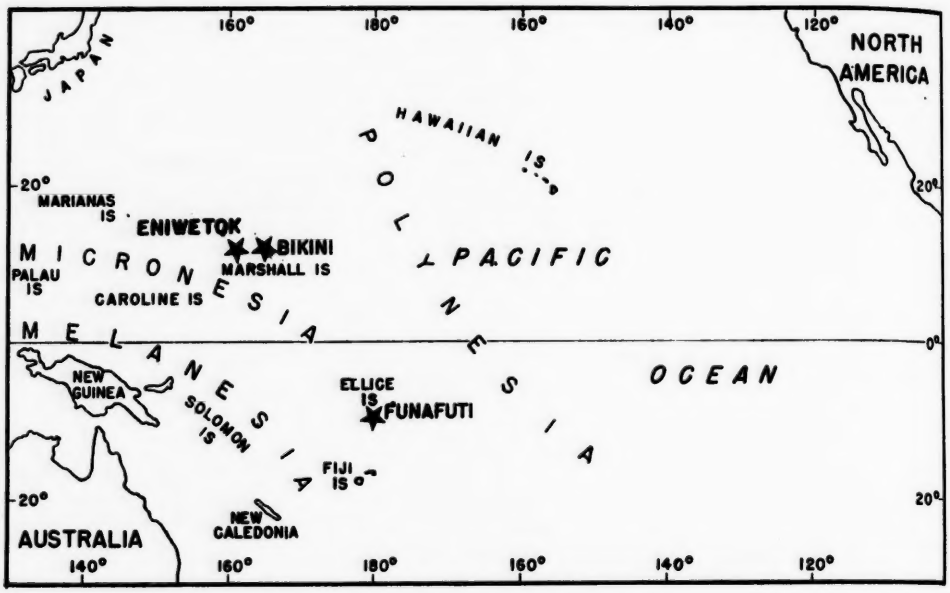
(All figures are camera lucida drawings except figures 2 and 5 which are unretouched photographs.)

FIGS. *1–6—Ptychodon inexpectans* n. sp. *1,3,6*, holotype, USNM 562088, ×23. *4*, paratype B, USNM 562089B, ×23. *2,5*, paratype A, BM73490, ×13 and paratype B, USNM 562089B, ×13; showing color pattern.

7,8—Ptychodon subpacificus n. sp., holotype, USNM 562090, ×23.

9–12—Ptychodon eniwetokensis n. sp., holotype USNM 562091, ×23.

13–15—Ptychodon species A, ×23.



TEXT-FIG. *1*—Index map.

As Pilsbry pointed out long ago, the existing land snail faunas of the Pacific islands may be divided into two groups: one group lives on low islands and the shore zones of high islands, the second group inhabiting the forests of high islands (Pilsbry 1916, p. 429). The endodonts, including the fossil species here described, belong to the second group.

A "subfossil" endodont was described from New Zealand, the species occuring in a Recent sea-beach deposit (Murdock and Finlay, 1923). Several species from the isolated island of St. Helena in the South Atlantic are known only from dead shells and are believed to be extinct (Smith, 1892). The species here described appear to include the first true fossils in that at least 3 of the 4 are pre-Recent in age.

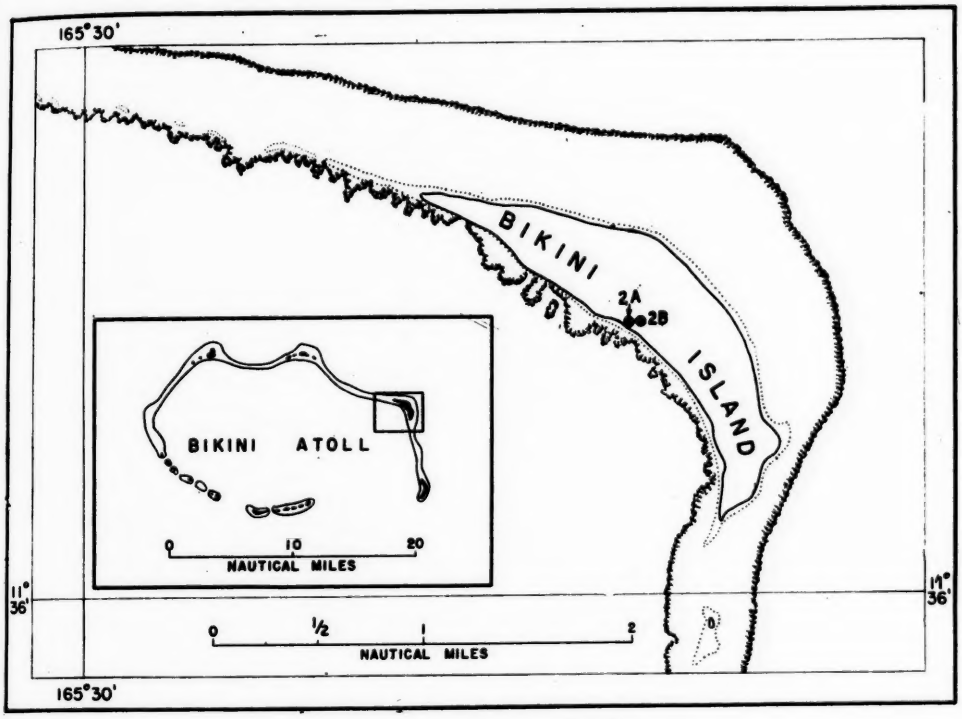
The fossils have been compared with material in the collections of the U. S. National Museum, the Academy of Natural Sciences in Philadelphia, the Museum of Comparative Zoology, and the Bernice P. Bishop Museum. Some species that originally were only briefly described have never been figured and in a few such cases no specimens were available for comparison. Endodonts, including *Ptychodon* as here recognized, are represented by many species in Polynesia. Zimmerman (1948, p. 102) noted that in Hawaii alone 25 species and one subspecies have been described and he cited the belief of the late Dr. C. Montague Cooke that if all the material that has come to the Bishop Museum in the last 25 years was described the total for Hawaii would exceed 100 species. The present inquiry is concerned only with the group of minute species in which the aperture bears lamellae such as those exhibited by the fossils.

LOCALITIES

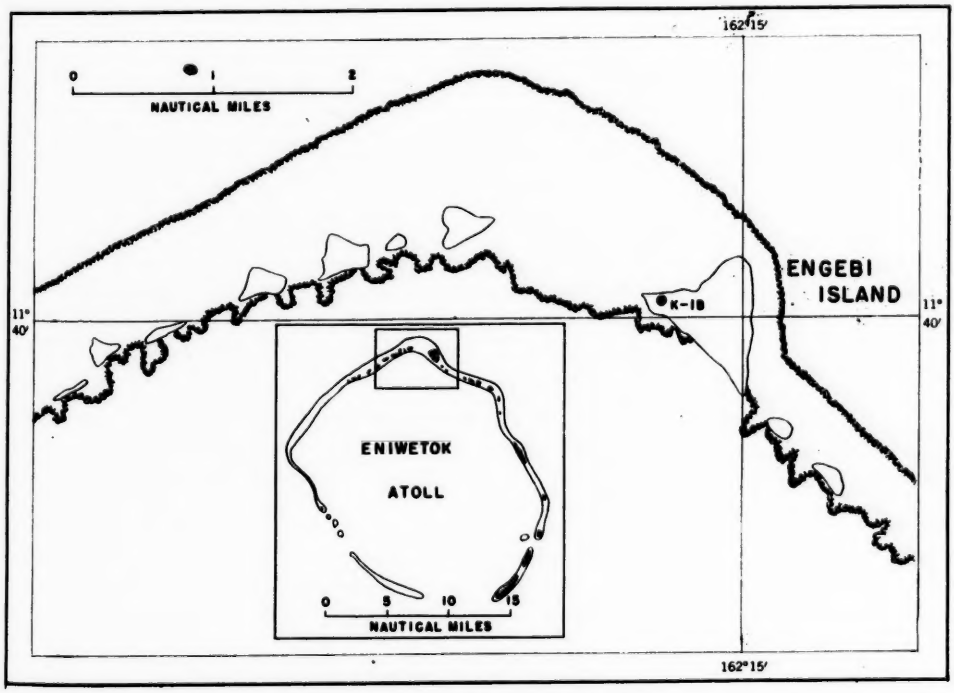
The drill holes that yielded the fossils are all located on islands on the windward sides of their respective atolls. On Bikini and Eniwetok the holes are on the lagoon side of the islands (Text-figs. 2,3), on Funafuti the hole is on the sea side (Text-fig. 4).

NATURE OF OCCURRENCES

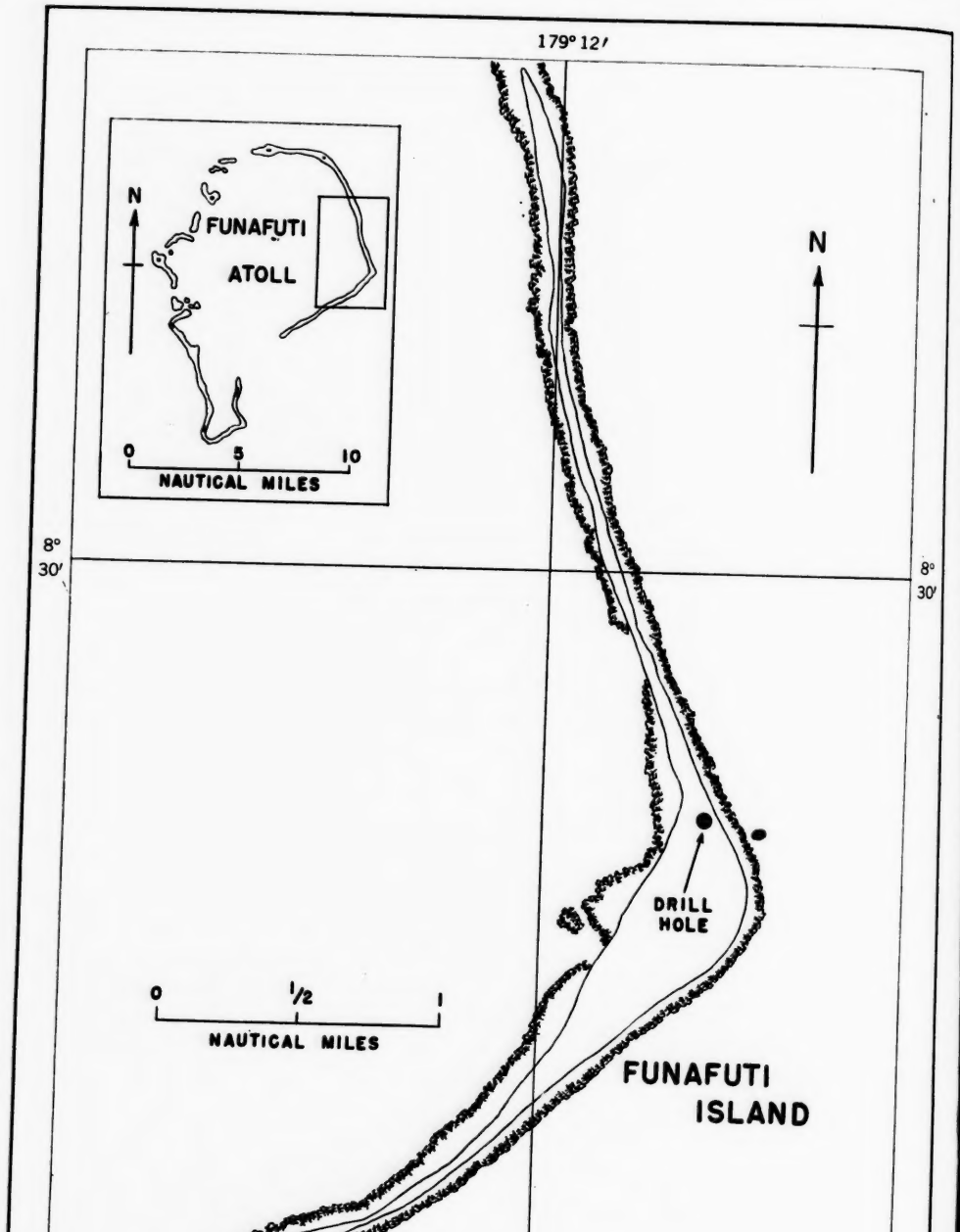
All of the land shells from the drill holes were picked from cuttings, none having been found to date in any of the cores. Shells as small as these can, of course, circulate in the drilling fluid, particularly if the fluid be a heavy mud. Under these conditions there is, admittedly, some doubt as to the exact



TEXT-FIG. *2*—Sketch map of Bikini.



TEXT-FIG. *3*—Sketch map of Eniwetok.



TEXT-FIG. 4—Sketch map of Funafuti.

depth from which the shells were obtained. They could have fallen into the hole by the caving of sediments already penetrated by the drill or they could have circulated in the drilling fluid to be recovered from depths appreciably greater than those from which they were derived. They are, however, true fossils and do not represent the shells of living forms that dropped into the open hole or were pumped in from the mud pits. The 7 specimens of *Ptychodon inexpectans* were recovered from a sack of cuttings taken from a 5½-foot section of a 6-inch drill hole 2A on Bikini (447–453 feet). None of the cuttings from higher or lower levels yielded any specimens of this shell and the fact that 7 specimens were recovered from the one sample would seem to be an indication of great abundance at that particular spot. Drill hole 2B located only 179 feet away yielded no shells of this species. The specimens recovered are well preserved and retain traces of original color but the interiors of the tiny shells and the umbilicus of some are tightly filled with a calcareous matrix that seems to establish their fossil nature clearly. Furthermore, no endodonts of this type were found either alive or dead among the collections of surface shells made on the atoll by J. P. E. Morrison (verbal communication, 1956). Two specimens of Recent land shells were recovered from cuttings at Bikini, one from a depth of 232–243 feet in hole 2A and one from a depth of 1219–1230 feet in hole 2B. Both of these specimens are fragile and unfilled and are identical with shells collected on the surface. They probably were pumped into the hole from the mud pits.

The two specimens of *Ptychodon* obtained from Tertiary strata (*P. subpacifica* and *P. eniwetokensis*) at depths of hundreds of feet in holes on Bikini and Eniwetok are incomplete and this may indicate that they traveled for some time in the drilling mud before being recovered. They may belong to higher horizons than those recorded but they are clearly Miocene in age as they exhibit the light brown coloration that characterizes other fossils from the Miocene sediments. The single specimen from Funafuti (166–170 feet) is delicate and unfilled but shows no color other than a trace of iron stain which Hinde credited to the drilling apparatus while noting that the organisms from this interval had lost their fresh appearance (Hinde 1904, p. 209).

ACKNOWLEDGEMENTS

I am indebted to the British Museum (Natural History) and the Museum of Comparative Zoology for the loan of samples obtained from the deep hole drilled on Funafuti. R. Tucker Abbott of the Academy of Natural Sciences in Philadelphia, William J. Clench of the Museum of Comparative Zoology, Yoshio Kondo of the Bishop Museum, A. W. B. Powell of the Auckland Institute and Museum and Henry van der Schalie of the University of Michigan kindly sent type specimens and other material representing living species of *Ptychodon* for comparative studies. Lawrence B. Isham of the U. S. National Museum made all of the enlarged drawings shown on Plate 1. Harald A. Rehder and J. P. E. Morrison of the U. S. National Museum, Alan Solem of the Chicago Natural History Museum, and Joshua I. Tracey, Jr. of the U. S. Geological Survey read the manuscript critically and gave valuable suggestions.

SYSTEMATIC PALEONTOLOGY

Family ENDODONTIDAE

Genus PTYCHODON sensu lato

All of the fossils belong to a group of living Pacific species placed in the section *Thaumatodon* of the genus *Endodonta* by Pilsbry in 1893. Pilsbry designated no type for this group though in his introductory remarks he cited *Endodonta multilamellata* Garrett (Rarotonga, Cook Islands) and *E. derbesiana* Crosse (New Caledonia). In 1913 Suter gave *Thaumatodon* subgeneric rank and designated *E. multilamellata* as the type. In the same year Iredale also made this designation (1913, p. 376). Pilsbry pointed out (1893, p. 26) that the outer lip of *E. multilamellata* exhibits peculiar structures—long, curved, hook-like processes directed toward the aperture. These structures are not found in other species of the group and the choice of type seems an unfortunate one. Possibly the Pacific species placed in *Thaumatodon* by Pilsbry and the fossils here described should be assigned to one or more distinct subgenera. The spirally sculptured protoconch of *P. eniwetokensis*, for example, also characterizes several Recent species

that can be placed in the subgenus *Beilania*, type *P. inopina* Preston, a Recent species from Indonesia (Preston, 1913, p. 443). Pilsbry (in Pilsbry and Ferriss, 1906, p. 154) also used this character to define the genus *Radiodiscus* among the non-toothed endodonts. In the present paper, all of the fossil species are referred to *Ptychodon* s.l., using this term to include all toothed endodonts. The group is widely distributed in the Pacific today (Solem, 1957) and apparently has been represented in some parts of the area at least since early Miocene time. In proposing *Ptychodon* as a generic name, Ancey (1888, p. 372) designated *Strobila leiodus* Hutton, a Recent New Zealand species, as the type. In the key that follows, the fossil species are contrasted with their living relatives. In this arrangement the importance of the parietal lamellae may have been overemphasized. If more specimens of both Recent and fossil species had been available, the number and structure of these lamellae might have appeared more variable and less trustworthy a criterion for specific determination.

KEY TO FOSSIL (†) AND RELATED RECENT SPECIES OF *Ptychodon*

- Initial whorls spirally ribbed
  - Parietal lamellae two ..... †*P. eniwetokensis*
  - Parietal lamellae one ..... *P. philippinensis*
- Initial whorls smooth or costate
  - Adults whorls coarsely costate; growth threads well developed between costae
    - Last whorl with not more than 40 costae ..... *P. henshawi*
    - Last whorl with 60 or more costae
      - Parietal lamellae three ..... *P. royanus*
      - Parietal lamellae two
        - Lamellae on outer lip present ..... *P. thwingi*
        - Lamellae on outer lip absent ..... *P. consimilis*
      - Parietal lamellae one, bifid
        - Reddish brown, flammulate ..... *P. pseutes*
        - White ..... *P. amandus*
  - Adult whorls finely costate, without well developed growth threads between costae
    - Spire flat or depressed
      - Whorls flattened at periphery ..... †*P. subpacificus*
      - Whorls rounded peripherally
        - Umbilicus less than one-third diameter of shell ..... *P. nuda*
        - Umbilicus wide, nearly one-half diameter of shell ..... †*P. species A*
    - Spire elevated
      - Parietal lamellae four ..... *P. daedalea*
      - Parietal lamellae three
        - Parietal lamellae strong, equal in length ..... †*P. inexpectans*
        - Parietal lamellae weak, lowest one short ..... *P. rarotongensis*
      - Parietal lamellae two ..... *P. parvidens*

PTYCHODON INEXPECTANS Ladd, n. sp.
Pl. 30, figs. 1–6

Shell small, spire low, composed of 4¼ rounded whorls separated by a well impressed suture; last whorl descending to a lunate aperture; apex smooth, adult whorls costate, the last bearing about 145 closely spaced ribs that curve backward below the periphery in a shallow saddle; umbilicus narrow, equal to about one-fourth the diameter of the shell; whorls within umbilicus convex. Aperture provided with 3 strong, spirally entering parietal lamellae, of equal length, that increase progressively in height, the uppermost one being the highest, and two moderately strong basal lamellae. Outer two and one-half whorls crossed by 20 or more fairly regularly spaced orange-brown bands separated by equal or slightly wider interspaces (pl. 1, figs. 2,5).

Diameter of holotype (USNM 562088) 2.1 mm., height 1.1 mm. Paratype A deposited in the British Museum (B. M. 73490). This specimen and five other paratypes (USNM 562089B–562089F inclusive) are essentially the same in size.

Occurrence.—In limestone cuttings from Drill Hole 2A on Bikini Island, Bikini Atoll, Marshall Islands at a depth of 447 to 453 feet. The land shells are associated with a diversified fauna of shallow water marine mollusks that is definitely post-Miocene, probably Pliocene. The land shells probably were brought in at a later date when the

marine limestone was above the sea undergoing solution and recrystallization; the land shells may be Pleistocene.

The closest relative of *P. inexpectans* is *P. rarotongensis* (Pease)[2] from the Cook Islands. This species has never been figured but comparison was made with a specimen from the Museum of Comparative Zoology (No. 161553) identified by the late C. Montague Cooke. *P. rarotongensis* is larger (diameter 2.8 mm., height 1.3 mm.) and more coarsely sculptured. The last whorl bears only 125 costae and under high magnification faint traces of growth threads can be seen between the costae. The three parietal lamellae of the Recent shell are noticeably weaker than those of the smaller fossil, the lowest one being short and lying well within the aperture. The single Recent shell carries 4 other lamellae—a weak one on the columella and 3 somewhat stronger ones on the outer lip. In his original description Pease mentions 3 parietals and 2 others. In a later description (Pease, Proc. Zool. Soc. London, p. 453, 1871) only 2 parietals are noted.

Other species that, superficially at least, resemble *P. inexpectans* are: *P. daedalea* (Gould) from Makatea in the Tuamotu Group, *P. parvidens* and *P. consimilis* described by Pease from the Society Islands, *P. henshawi* and *P. thwingi* described by Ancey from Hawaii and *P. royanus*, *P. amandus*, and *P. pseutes* described by Iredale from the Kermadec Islands. Important differences between these species and *P. inexpectans* are given in the key.

PTYCHODON species A
Pl. 30, figs. 13–15

Shell small, flatly coiled, spire depressed near apex, consisting of three and a half rounded whorls separated by a well impressed suture; last whorl descending to a broadly lunate aperture; apex and first one and a half whorls smooth, remaining whorls crossed by close-set, prominently elevated costae that are more closely spaced near the aperture than on earlier parts of spire; from the periphery the costae are deflected slightly backward; last whorl bears 70 costae; umbilicus broad and shallow, equal to nearly half the diameter of the shell; whorls within umbilicus broadly rounded and separated by a deep suture. Aperture (slightly broken) provided with two strong parietal lamellae, three basal plicae, and one columellar la mella.

Diameter 1.4 mm., height 0.7 mm. Known from a single specimen obtained from the part of the Funafuti core that is on deposit at the British Museum (Natural History) in London. The writer desires to express his thanks to authorities of the British Museum for the loan of the Funafuti samples. Unfortunately after the shell had been described and figured the single specimen disappeared. Pending its recovery or the finding of a second specimen the specific name originally attached to it has been suppressed.

Occurrence.—In partially leached, coralliferous limestone from the deep boring on Funafuti Atoll, Ellice Islands, at a depth of 166–170 feet. Age Pleistocene or Recent.

Ptychodon species A seems most closely related to *P. nuda* (Ancey), a Recent Hawaiian species. The fossil is less than half the size of the Recent shell and has a wider umbilicus. I have not seen specimens of *P. nuda* but Ancey's figures (1899 Proc. Mal. Soc. London, vol. 3, p. 268, pl. 12, fig. 1) do not suggest that the costae near the aperture are more closely spaced than elsewhere. There may likewise be differences in the lamellae of the outer lip.

PTYCHODON SUBPACIFICUS Ladd, n. sp.
Pl. 30, figs. 7,8

Shell small, spire almost flat, composed of 4 rounded whorls that are slightly flattened at the periphery; suture distinctly impressed; last whorl descending; aperture ovate, narrower above; initial whorl faintly costate; costae of adult whorls are directed backward; earlier half of last whorl bearing

[2] Described as "*Pithys roratongenesis*" from "habitat in insula Roratonga" (Pease, W. Harper, 1870, Remarques sur certaines espèces Coquilles terrestres habitant la Polynésie, et description d'espèces nouvelles, Jour. de Conchy., vol. 18, p. 395,396). This is an error in spelling. Williams, the European credited with discovery of the island, called it Rarotonga (Williams, John, 1837, Missionary enterprises in the South Seas, p. 108) and this is the accepted spelling today. Actually, according to Gould, 1881, Jour. Acad. Nat. Sci. Phil., 2nd ser., vol. 8, p. 290), the types of *P. rarotongensis* were collected by him on Atiu, an island near Rarotonga.

about 40 costae; umbilicus less than one-third of the diameter of the shell (partly filled with fine, cemented limestone particles in holotype); interior with two strong spiral lamellae; outer lip not preserved on holotype.

Diameter of holotype (incomplete), U.S.N.M. 562090, 1.8 mm., height 0.7 mm.

Occurrence.—In cuttings from drill hole 2B on Bikini Atoll at a depth of 1807 to 1818 feet; age lower Miocene (Miocene *e*).

Though the holotype is incomplete, a name for the specimen seems justified. If the fossil had been obtained from an outcrop from which more complete specimens might later be collected, the writer would be loath to designate a single incomplete specimen as a type. It is unlikely, however, that additional material will be recovered from drill holes in the western Western Pacific in the near future.

P. subpacificus is larger than *Ptychodon* species *A* and has a narrower umbilicus; its whorls are flattened peripherally and the costae are more strongly deflected backward on their upper surfaces.

PTYCHODON ENIWETOKENSIS Ladd, n. sp.
Pl. 30, figs. 9–12

Shell small, spire flat, whorls rounded, suture deeply impressed, umbilicus narrow, equal to about one-fourth the width of the shell. Initial whorls marked by 8 or 9 faint spiral ribs, adult whorls crossed by fine costae, the penultimate whorl with about 90; on the adult whorls, under high power, faint, close-set spiral threads may be seen crossing the grooves between costae. Parietal wall with two strong lamellae, armature of outer lip unknown.

Diameter of holotype, U.S.N.M. 562091, incomplete, 1.8 mm., height 0.8 mm.

Occurrence.—In limestone cuttings of upper Miocene (Miocene *g*) from drill hole K-1B on the island of Engebi, Eniwetok Atoll, at a depth of 820–831 feet. The single specimen on which the above description is based is the only endodont obtained from Eniwetok Atoll though more drilling has been done there than on any other atoll. The holotype is incomplete, lacking most of the last whorl and revealing no apertural features other than the parietal lamellae preserved on the penultimate whorl. It shows distinctive features, however, and the chances of obtaining better type material from the area are remote.

The presence of spiral sculpture on the protoconch places this species in the subgenus *Beilania* (type *B. inopina* Preston, 1913). In this same group are the Recent species *P. philippinensis* (Semper) from the Philippines, *P. heptaptycha* Quadras and Möllendorff from Guam, also an unidentified Pleistocene(?) species from Palau. *P. eniwetokensis* is slightly larger than *P. philippinensis* and has a narrower umbilicus. The two are generally similar in shape and sculpture but the fossil has two strong parietal lamellae, the Recent shell only one. The Guam and Palau species have 4 and 5 parietal lamellae respectively.

ECOLOGY

Distribution.—Living species of the group to which the fossils belong (sections *Thaumatodon* and *Nesophila* of Pilsbry, 1893, p. 26–27) are widely distributed today in Polynesia and Australasia. Pilsbry listed 44 species from Polynesia along with 9 from New Zealand, New Caledonia, Tasmania, and the Philippine Islands. In a closely allied group—*Ptychodon* Ancey, 1888—Pilsbry listed 7 additional forms (pp. 27–28), all from New Zealand. Pilsbry, likewise, noted that there were 8 closely related species from St. Helena. These he grouped in the section *Helenoconcha* (p. 28), stating that since the soft parts were not known this was a tentative action, based largely on their distribution.

The lower Miocene species from Bikini resembles the Quaternary fossil from Funafuti and a species now living in Hawaii. The upper Miocene species from Eniwetok seems to be most closely related to a form now living in the Philippines. The post-Miocene species found in comparative abundance under Bikini has its closest relative in the Cook Islands but it closely resembles other species in several island groups, from Hawaii on the north to the Kermadecs on the south.

So far as the writer has been able to determine, no fossil endodonts have been described previously from the Pacific even from the richly fossiliferous beds of Java. Miss Jutting reviewed the known occurrences of fossil non-marine mollusks in Java,

noting (Jutting, 1937, p. 171) that the lower Pliocene and older horizons had never yielded any land or freshwater mollusks. This led to the opinion that the non-marine mollusks were a young element in the natural history of Java.

Habitats.—Published records and the data accompanying collections indicate that living representatives of the group under consideration thrive on high islands where wooded mountains and valleys provide damp leaf mold and rotting wood.

Existing atolls with their limited growth of trees and consequent paucity of rotting wood and leaf mold are not favorable for endodonts. As previously noted, no endodonts of any kind were found on the atolls of the northern Marshalls during the surveys accompanying Operation Crossroads. Hedley found no shells of toothed endodonts when he collected on Funafuti but he did refer (Hedley 1899, p. 488) to a species, *Endodonta decemplicata* Mousson (Mousson, 1873, p. 105) reported in abundance by Graeffe from two Ellice atolls lying north of Funafuti—Nukufetau (Island De Peyster) and Vai-Tupu (Tracy Island). Hydrographic charts of these two atolls show no elevations but presumably both are low. *E. decemplicata* has never been figured but its armature is quite different from those of the fossils here described.

When the Wilkes Expedition visited Makatea (Metia, Aurora, Matea) in the Tuamotu (Paumotu) Archipelago in 1839 (Wilkes, 1845, p. 351–356) a number of land shells were collected, including a *Ptychodon*. This form was later given the name of *daedalea* by Gould who reported that it was abundant under stones (Gould, 1862, p. 54–55). At a later date Cooke (1935, p. 5) identified many dead shells of this species from Makatea from soil pockets in coral rock at an elevation of 250 feet and in moss growing on the rock at elevations of 250 and 300 300 feet. *P. daedalea* resembles *P. inexpectans* and the occurrences show that shells of the type under discussion can live on elevated limestone islands.

In Hawaii, where toothed endodonts have been extensively collected, living shells are limited to wooded mountainous areas where some species live on the ground associated with rotting wood, and other live on trees. Some species that are known only from Recent "fossil" collections lived on the coastal plain at lower levels but this, apparently, was in past times when the forest cover extended to such levels (Cooke, 1928b, p. 14). A general survey of Polynesian occurrences shows clearly that the shells prefer high islands where environments comparable to those known in Hawaii exist. Unfortunately, many of the described species bear no data about the environments other than the name of the island from which the species was collected.

The dependence of toothed endodonts on a forest cover appears to be well illustrated on the island of St. Helena. In 1892 when Edgar A. Smith reviewed and described the land shell fauna be noted that the destruction of the original forest cover had brought extinction to two-thirds of the 27 indigenous species (p. 259). Of 8 toothed endodonts, only 1 was reported to be still alive.

Many land shells are colonial and over a limited area occur in abundance. It seems doubtful, however, that the shells of *P. inexpectans* were alive when buried. The recovery of seven specimens from a single sack of cuttings suggests that the drill penetrated a concentration of dead shells brought, perhaps, by rain wash, into a protected pocket. Such concentrations of dead shells are extremely common. In 1904 Henshaw described deposits of "semi-fossil" land shells from the island of Hawaii where they were scattered over an area of a few hundred square yards. At one of the localities the shells occurred in a horizontal layer two or three inches thick under a foot of humus (Henshaw, 1904, p. 28). In 1925 when the writer visited the Ewa coral plain west of Pearl Harbor on Oahu he noted that thousands of small dead land shells completely covered the ground in many places.

The occurrences of fossil land shells in the leached and recrystallized limestones of Bikini and Funafuti can, perhaps, be compared to conditions known to exist today on elevated limestone islands. On the island of Koror in Palau, for example, a small sack of limestone rubble collected from a fissure in the Palau limestone by Charles Johnson of the Geological Survey was rich in several species of land shells including more than 40 specimens of an undescribed *Ptychodon*.

The sample—comparable in size to the Bikini drill samples—was collected from an abandoned quarry 20 to 25 feet above sea level near the shore of the existing lagoon. On two sides of the quarry site wooded limestone ridges rise to heights of several hundred feet.

Murdock and Finlay (1923) described *Ptychodon suteri* from a Recent sea-beach deposit on South Island, New Zealand. The minute endodont was represented by many specimens and was found with 9 other species of land mollusks and many marine shells at the highest margin of the strand. The deposit was 130 feet long with a maximum thickness of 3 feet. The authors suggested that the land shells were contributed by a nearby creek.

In a collection of marine shells and fragmentary reef corals made by C. L. Rogers of the U. S. Geological Survey from an uncemented beach deposit forming a platform 5 to 8 feet above high tide on Peleliu in the Palau Group, the writer found one specimen of a toothed endodont. This solitary occurrence shows that on a forest limestone island like Peleliu (maximum elevation about 250 feet) shells of this type are carried to the beach unbroken and become buried with an assemblage of shallow water marine mollusks.

MODES OF DISPERSAL

As previously mentioned, living relatives of the snails here described are found mostly on high islands where they favor damp forested areas with leaf mold and rotting wood. Such living habits are restrictive and travel from one forested area to another or from one island to another is difficult. As pointed out in the discussion of distribution, however, it is clear that at some time in the past and by some means or other these minute shells have traveled extensively. The islands that they now occupy are separated in many instances by hundreds of miles of open ocean and there is no geologic evidence to indicate that these islands were ever connected. Years ago many zoologists looked with favor on land bridges between islands but most students of terrestrial mollusks now agree that some sort of "island hopping" has taken place in the past and may still be functioning. Baker, in his monographic study of the zonitid snails of Pacific islands, discounted the value of land shell distribution in connection with more extensive land connections. He favored an hypothesis of "adventitious dissemination" (1941, p. 361). It was suggested that additional high islands were called for and probably did exist (Zimmerman 1942, p. 283; Gressitt 1956, p. 14). The fossil land shells offer supporting evidence for the postulated islands.

Three of the agents of dispersal commonly called upon—migratory birds, drifting vegetation, and hurricanes—are briefly described below. Each of these three agents may have contributed to the dispersal of small snails. A fourth agent is man himself but man cannot be cited as an important agent in the distribution of the toothed endodonts since shells of this type were present on widely separated islands long before man entered the Pacific.

In considering means by which endodonts can be distributed, it must be borne in mind that they are exceedingly small (1½ to 2 mm.) and light and furthermore that in some members of this group the female carries the fertilized eggs in the umbilicus. If one such female with eggs could be transported to a favorable environment a new colony could be established. Any traveling snails that landed on unfavorable "stepping stones" (a category that includes most sea level atolls) would perish and leave no record.

Migratory birds.—The migratory habits of many Pacific birds are well known (Bogert, 1937; Stickney, 1943; Mayr, 1945). Some that breed in New Zealand and other austral areas winter among the Pacific islands; others that breed in Alaska and such boreal areas likewise winter in the islands or in New Zealand and Australia to the south. The flight patterns of a number of these birds coincide with the distribution of the types of land shells under consideration and the birds themselves use the islands as stepping stones (Mayr, 1945, p. 28). The living habits of these snails, however, make it seem unlikely that birds were a major factor in their distribution.

The snails under consideration are small enough to be carried entire in particles of mud that might adhere to the feet of a bird in its flight from one island to another. The

snails, however, are not shore forms inhabiting muddy flats were birds might pick up encrustrations of mud. Instead, they prefer forested valleys. These environments are not ordinarily muddy though the possibility of live snails being found (at least temporarily) on sticky areas of exposed volcanic mud cannot be entirely ruled out. Some sea birds, such as shearwaters, terns, and tropic birds nest in island forests from sea level to over 6,000 feet (Zimmerman 1948, p. 60) and thus could have close contact with tree living snails. The snails here considered are not operculate and thus cannot become locked to the feather of a bird in the manner described by Bondesen and Kaiser (1949, p. 268). The absence of an operculum would seem likewise to eliminate for these snails the possibility also mentioned by Bondeson and Kaiser (ibid, p. 270) of snails being carried to a new locality after being eaten by a bird or fish and then vomited or passed with the feces. Bondesen and Kaiser cited evidence to show that brackish water snails (hydrobids) can pass uninjured through the alimentary canal of certain fishes though not through others. These workers found experimentally that no snail would pass unbroken through the alimentary canal of a domestic duck.

The calcareous epiphragm that may be secreted during estivation might protect a snail temporarily if it were swallowed by a bird and snail eggs—carried in the umbilicus in the forms under consideration—might conceivably survive temporarily and be vomited prior to digestion. To the writer, however, these possibilities seem remote as regards transportation between islands that lie hundreds of miles apart. Both drifting vegetation and hurricane winds would seem to be more likely agents.

Drifting vegetation.—In earlier years, when many students of Pacific land shells looked upon hypothetical land bridges as the only satisfactory way of distributing the ancient stocks of land snails that occupy widely scattered islands, ocean currents and drifting vegetation were rejected as entirely inadequate. One leading member of the older school told the writer in 1926: "No! I've examined drifting logs after they have come ashore and no self-respecting land snail would live on one!" No doubt these observations are well-founded as far as individual logs are concerned but if the log has attached branches or if an entire tree is uprooted and carried to the sea the possibilities of transporting living land snails would be enhanced. A case from Tahiti was cited by Zimmerman (1942, p. 285). Emery (1955, pp. 52–53) described how both streams and marine erosion could bring trees into the ocean. In one instance a tree 3 meters in diameter was observed floating in a vertical position, its top 25 meters out of water, in the Gulf of Papua.

Ocean currents, including those produced by the wind at the surface, form complicated patterns but with persistent streams that in the tropical Pacific are capable of carrying drifting objects from one island to another over distances of tens or hundreds of miles at a maximum speed of 2 knots. The beaches of Fiji, for example, are littered with pumice from Tongan volcanoes that lie several hundred miles upwind to the southeast; on the beaches of the Marshall Islands, far removed from any centers of active volcanism, pumice occurs but rarely.

When the drift hypothesis is applied to the origin of island faunas surprising discrepancies or failures appear. Visher pointed out (1925, p. 71) that the prevailing Northeast Trades and the currents engendered by them should have given Hawaii many Californian and Mexican forms of littoral mollusks but such are not present. In the Indian Ocean the Southeast Trades blow with great strength and persistence from Australia to the Cocos-Keeling Islands but almost no Australian species are found in the island fauna (op. cit., p. 73).

Forest-loving snails like the Endodontidae are fastidious in the selection of a place to live. If unceremoniously cast upon a shore after an overwater drift they cannot be expected to make their way unaided to a suitable station. Natural rafting as an important factor in their distribution is still difficult to imagine. In Pilsbry's picturesque words: "Unless we imagine a natural raft stocked like Noah's ark for each island, we must suppose a long series of happy accidents for each individual island." (Pilsbry, 1921, p. 149).

Though natural drift by wind and current seems inadequate for land shell distribu-

tion, the sudden, irregular, and powerful winds associated with hurricanes and similar storms offer a more promising means of transportation—at least for minute shells like those under consideration. As Mayr pointed out, however, no thorough analysis of the relative efficiency of these two agencies has ever been made (Mayr 1953, p. 9).

Hurricanes.—The writer shares the opinion held by many (Gulick, 1932; Mayr, 1940) that air currents have been a far more important agent of distribution of life in the Pacific than sea currents. Tropical hurricanes travel long distances and have extraordinary lifting power. The lifting power of the main wind may not be great but there are gusts which seem to be secondary whirls (tornadoes) and these may have great lifting power (Darlington, 1938). Hurricanes have probably been the most effective agent in carrying small land mollusks to isolated spots such as Easter Island and St. Helena. Minute shells like those under consideration are light and they occur in large numbers. The powerful winds of a hurricane apparently can transport them as ordinary winds transport seeds. Cooke (1928a, p. 2280) expressed the opinion that the important agent for the distribution of small land shells in the Pacific was probably the hurricane.

PALEOECOLOGY

Island steppingstones.—In speculating about the origin of the Hawaiian insect fauna, Zimmerman (1948, p. 51–52) reasoned that many of the atolls lying south and southwest of Hawaii (including the Marshall and Ellice Islands) were once high islands that served as steppingstones for floristic and faunistic elements from Melanesian and southeastern Polynesian areas. When the postulated high islands were degraded or lowered to sea level they ceased to function efficiently as steppingstones because such life as persisted was handicapped by inadequate precipitation and the islands were subject to flooding by hurricanes and tsunami. Zimmerman pointed out that most atolls today are ecologic deserts, supporting few, if any, endemic land plants or land animals. In 1953 Mayr expressed his belief in the possible existence of high islands in what are now groups of sea level atolls (Mayr, 1953, p. 8).

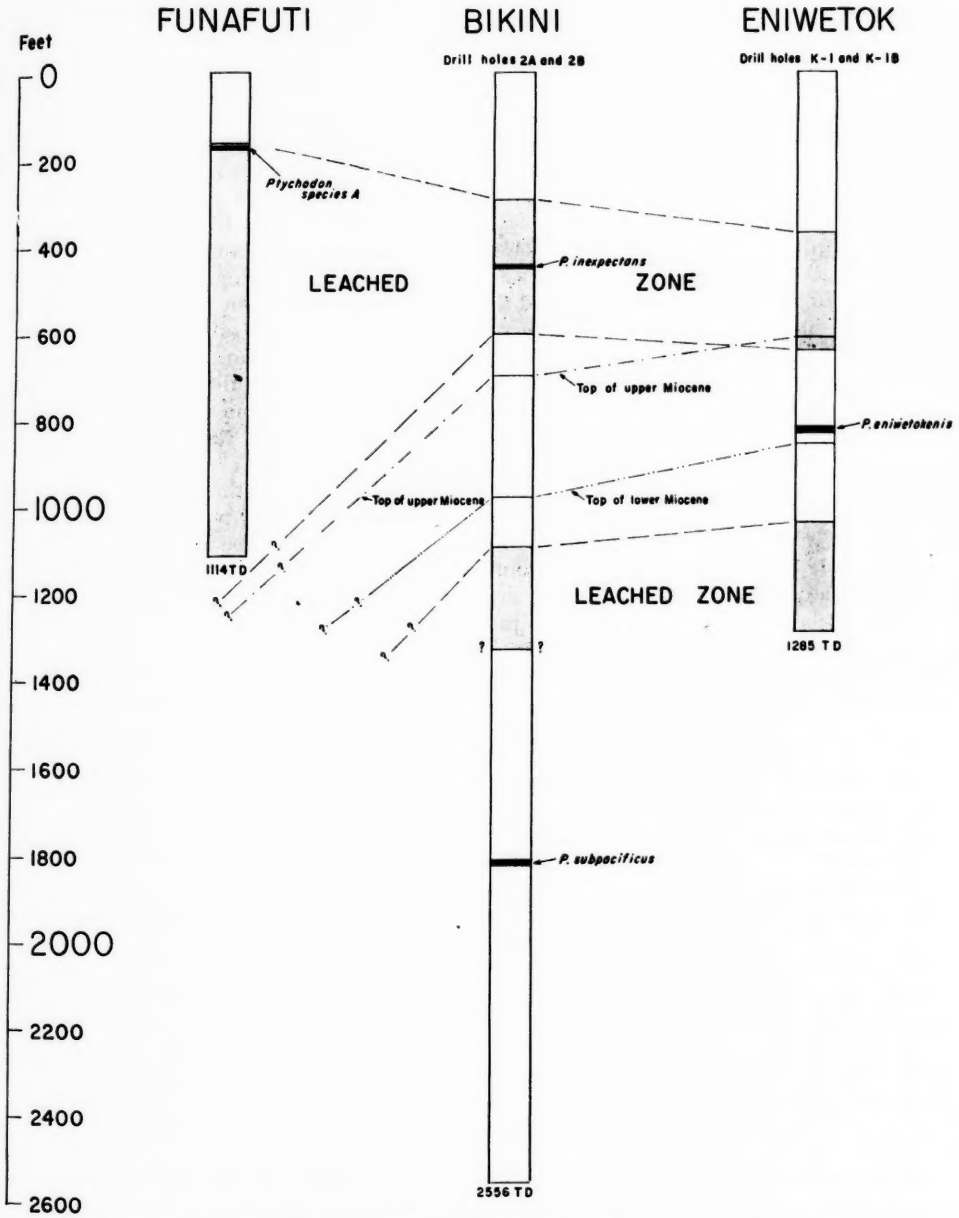
In a paper describing fossils dredged from Pacific guyots and in his excellent memoir on the sunken islands of the Mid-Pacific Mountains, Hamilton showed clearly that though a Pacific Ocean of appreciable depth existed in Cretaceous time there were, even then, a number of volcanic mounds that projected into shallow water and supported a rich marine fauna. The presence of erosional debris dredged from the break in slope and from the tops of the sunken volcanoes indicated that some of the structures probably projected above the sea and could have served as steppingstones for island life just as other islands seem to do today (Hamilton, 1953, p. 204,206; 1956, p. 29,51,53,55).

Evidence indicating that land plants existed on Eniwetok Atoll in Tertiary times has been found by Miss Estella B. Leopold of the Geological Survey. Moderate to very dense concentrations of pollen along with spores and other types of plant material have been recovered from depths of 810 to 880. The pollen occurences are comparable to those found today in shallow waters close to land. Miss Leopold states that the plant families present—with the exception of the palms—are those found only in a dense tropical deciduous forest. Such assemblages are not found in sediments deposited near a thinly vegetated atoll. Pollen gains have also been obtained from lignitic crusts in lower Miocene sediments at a depth of 2240-2450 feet but the grains are very rare in the samples examined to date. Miss Leopold is continuing her investigations and will report fully on her findings later.

Seismic studies and dredging and drilling operations in the northern Marshall Islands have furnished data which suggest that some of the present-day guyots and the foundations of existing atolls projected above the sea in late Mesozoic or earliest Tertiary time (Raitt, 1954, p. 507; Emery, et al., 1954, p. 131; Ladd, et al., 1953, p. 2278). Such islands may have functioned as steppingstones long before the limestones carrying the oldest fossil endodonts were deposited.

Emerged reefs.—Cores and cuttings obtained from drill holes on Funafuti and in the Marshall Islands have revealed zones in which the aragonite of corals and most

mollusks has been largely leached or recrystallized to calcite. Some of the molds resulting from the leaching have been partly or completely filled with calcite. Alteration of this sort can be accomplished under atmospheric conditions but not by ordinary marine waters for they are saturated with calcium carbonate and unable to dissolve limestone except under the specialized conditions found at intertidal levels. The



TEXT-FIG. 5—Diagrammatic sections of drill holes showing relations of land shell occurrences to zones of leaching.

leached zones are thought, therefore, to record periods when the tops of the atolls stood above the sea for appreciable periods of time (Ladd, Tracey, and Lill, 1948, p. 52; Fairbridge, 1950, p. 384, 393; Ladd, et al., 1953, p. 2278; Emery, et al., 1954, p. 2, 133; Ladd and Tracey, 1957. In the deepest holes drilled on Eniwetok there are three leached zones, the deepest hole on Bikini shows two, Funafuti only one. Some of these zones are indicated in Figure 5; age boundaries are based largely on determinations of larger Foraminifers made by W. Storrs Cole (Cole, U. S. Geological Survey, Prof. Paper 260-V, in press).

On Funafuti, as noted by Hinde (1904, p. 191, 210), the aragonite of corals below a depth of 180 feet has been dissolved and the interstices filled with calcite. The top of the leached zone actually occurs at least 20 feet higher. Hinde himself reported "casts and fragments" of corals in sample 143 from a depth of 166–170 feet (op. cit. p. 209). This is the sample that yielded the land shell. The present writer found molds of minute mollusks in it and in sample 142 obtained immediately above at a depth of 160–166 feet. Sample 143 also contained two minute marine mollusks in which the original shell appears to be preserved. For practical purposes the top of the leached zone can be drawn at 160 feet (Fig. 5). As in the case of the Bikini hole, the leaching would seem to record a time when the top of the atoll stood above the sea. Near the end of the emergent stage *Ptychodon sp.* A lived on the island and its unaltered shell was buried in the recrystallized calcitic rocks when submergence was resumed.

The limestones from which the Bikini and Eniwetok land shells were obtained are believed to represent lagoon deposits (Emery, et al., 1954, p. 90–91; Ladd, et al., 1953, p. 2278). The limestone from Funafuti from which *Ptychodon* sp. A was obtained may well belong in the same category. Grimsdale, who reviewed earlier work in a reappraisal of the Funafuti record, agreed with some of the earlier workers that the rocks to a depth of 550 feet pointed to reef core and/or lagoonal deposits (Grimsdale, 1952, p. 7). Lagoons may have disappeared, at least temporarily, during periods when the tops of the atolls stood above the sea. During Miocene time when the shells of *P. subpacificus* and *P. eniwetokensis* were deposited with varied assemblages of marine shells some sort of lagoon probably was present adjacent to the islands on which the endodonts lived. *P. inexpectans* and *P.* sp. A were probably lodged in crevices in elevated lagoonal limestone while they were above the sea undergoing subaerial erosion.

The emergent stages that interrupted the overall history of submergence in pre-Pleistocene time in the western Pacific may have been caused by local changes. In figure 5, the section drilled on Funafuti is all post-Miocene and this section is nearly twice that found under Bikini and Eniwetok. The post-Miocene section on Eniwetok is only slightly thinner than that of Bikini but on Jaluit Atoll, in the same island group, Miocene fossils were found in pebbles in blocks of coral conglomerate thrown up on a reef flat by waves (Yabe and Aoki, 1922). This occurrence suggests that the Miocene lies much higher there.

The duration of the periods of emergence and the exact heights of the emerged parts of the reefs cannot be determined accurately because unknown amounts of limestones may have been removed by subaerial erosion.

BEARING ON SUBSIDENCE THEORY

The deep drilling that has been done on coral islands in the Pacific confirmed a main postulate of Darwin's subsidence theory for the origin of coral reefs by indicating clearly that the overall history of the areas drilled has been one of subsidence. Coralliferous limestones of reef origin totaling hundreds and even thousands of feet were drilled and these depths far exceed the maximum depths at which the more important reef builders can flourish. The deepest of the drill holes—those on Eniwetok Atoll in the Marshall Islands—confirmed a second postulate, namely that the thick cap of reef rock rests on the summit of a volcano. Textbook versions of the subsidence theory postulate a slow and *continuous* subsidence but drilling data and the occurrence of the land shells here described suggest that several stages of emergence interrupted the long history of subsidence.

In the drill holes, zones containing arago-

nite are separated by zones in which aragonitic shells and skeletons have been partially leached or recrystallized to calcite. Aragonite is a less stable form of calcium carbonate than calcite and under ordinary atmospheric conditions tends to be converted into calcite (Johnston, Merwin, and Williamson, 1916, p. 509, 510). The time necessary to effect a conversion under subaerial conditions is not known definitely. On Guam, Schlanger noted that (Schlanger, S. O., written communication, 1956) small pockets of aragonite-rich limestone have persisted in otherwise almost completely recrystallized limestone deposits several hundreds of feet thick and several miles in lateral extent. These rocks though post-Miocene in age have apparently been above sea level for some time. From this Schlanger concludes that, whereas recrystallization suggests emergence, the mere presence of aragonite in a drill core "should not be taken as unequivocal evidence for a history of non-emergence." Nonetheless, the preservation at Bikini and Eniwetok of a considerable section of lower Miocene limestone in which abundant aragonitic organic remains are unaltered does suggest that these sediments have never been exposed to prolonged subaerial erosion. The aragonite has been stable under these submarine conditions for some tens of millions of years. The occurrence above and below such aragonitic zones of a thick section of pre-Miocene and post-Miocene sediments in which the aragonitic shells have been largely removed or recrystallized to calcite suggests that the leached parts of the section stood above sea level for appreciable lengths of time (Emery, et al., 1954, p. 2).

Drilling likewise revealed evidence of minor shifts in the relations of land and sea that probably are tied to Pleistocene glaciation (Emery, et al., 1954, p. 133). The occurrence of *Ptychodon* sp. A in a leached zone under Funafuti at a depth of 166–170 feet probably is related to such a Pleistocene change of level. During the glacial epochs the top of the atoll stood above the sea and its limestones were modified by solution and recrystallization.[3] *P.* sp. A probably lived on the land during such an emergent epoch and was buried later by the rising waters. These Quaternary fluctuations were not envisaged by Darwin though they fit perfectly into later versions of the subsidence theory and, of course, are easily explainable by almost any version of the glacial control theory.

[3] Several workers have suggested that the present-day reefs of the Pacific are growing on eroded limestone topography (MacNeil, 1954, p. 403).

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POLYSPORIA MIRABILIS NEWBERRY, A FOSSIL LYCOPOD CONE

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ABSTRACT—Examination of the holotypes of the fossil lycopod cones *Polysporia mirabilis* Newberry 1873, *Lepidophyllum truncatum* Lesquereux 1879 and *Lepidostrobus* (*Macrocystis*) *truncatus* Lesquereux 1884 has shown all three to represent the same species as the British fossil recently described by the author as *Lepidostrobus zea*. The cones prove to have important characters distinguishing them from typical *Lepidostrobus*. Newberry's genus *Polysporia* is emended, and these and other specimens are assigned to a single species, *P. mirabilis*. The megaspores contained in these cones are of the type known as isolated spores under the name *Valvisporites auritus* (Zerndt) Potonié & Kremp (1956), (*Triletes auritus* of Dijkstra 1946, and others). The contained microspores are closely similar to the type known isolated as *Endosporites globiformis* (Ibr.) Schopf, Wilson & Bentall 1944. The characters by which the genus *Polysporia* is distinguished from *Lepidostrobus*, *Sigillariostrobus* and other fossil lycopod cones are tabulated.

INTRODUCTION

FOSSIL lycopod cones are not among the commonest of Coal Measure plants, and those still containing spores are distinctly infrequent. They have long attracted the attention of paleobotanists, particularly since their connection first with *Lepidodendron* and later with *Sigillaria* demonstrated the fact that this group of large tree-sized plants was not gymnospermous as at first supposed, but reproduced by spores. Much of our knowledge of Carboniferous lycopod cones has been derived from petrifactions, which yield a good deal of information about the internal structure, but are rather rare and restricted to only a few localities and horizons. However, many compressions of fossil lycopod cones, apparently most unpromising in external appearance, yield beautifully preserved cutinized spore exines on maceration, although the bulk of the cone tissue has been broken down in the process of fossilisation. Many such lycopod cone compressions were described before the use of this maceration technique became widespread; indeed, few of the earlier paleobotanists investigated spore-containing cones by this method.

The great expansion in the use of both megaspores and microspores for stratigraphic purposes has renewed interest in the spores contained in fossil fructifications. Their study obviously offers a means of recognising what plant groups are represented by the isolated spores occurring in coals and other rocks. Work on these lines also forms a basis for a meaningful classification of isolated spores, and provides additional characters for identifying the fructifications in which they are found (e.g. Arnold 1938, Schopf 1941a,b, Felix 1954, Chaloner 1953b, 1953c, 1954).

Some specimens of a lycopod cone compression containing a rather unusual type of microspore were recently described from Britain (Chaloner 1953a). One of these specimens had been briefly described by Kidston (1897) as "*Sigillariostrobus* sp." A few years earlier, two very similar cone compressions had been described from the United States: *Polysporia mirabilis* Newberry 1873 and *Lepidostrobus* (*Macrocystis*) *truncatus* Lesquereux 1884. Although both Kidston and these American authors realized that their cones contained spores, they did not attempt to extract them or to examine them microscopically. Re-examination of the type-material of these two American species, and in particular the extraction of megaspores and microspores from them by maceration now shows that they are identical with the British specimens described as *Lepidostrobus zea*.

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the New York Botanic Garden for enabling me to examine and make preparations from the specimens on which this paper is based; and to Prof. Dr. R. Potonié for the constant interest that he has taken in this work, and for taking the photographs of pl. 32, figs. 4 and 5, and allowing me to reproduce them. My thanks are also due to the Commonwealth Fund of New York for granting me the Fellowship which made this work possible. I am also most grateful to Mr. R. Brinsden of the Botany Dept., University College, London, who took some of the photographs.

DESCRIPTION OF THE SPECIMENS

Four nearly complete cones of *Polysporia mirabilis* from which megaspores and microspores have been obtained are now known from Pennsylvania and Ohio, from Airdrie, Scotland, and from Yorkshire, England. In addition to these, detached sporangia are known from Pennsylvania, Illinois and Yorkshire.

The cones (pl. 31, fig. 7) are compressions in shale or clay-ironstone nodules, in a similar state of preservation to the specimens described as *Lepidostrobus zea*. The cone structure is basically that of all lycopod fructifications—an axis on which are arranged spirally more or less leaf-like sporophylls, close to the base, or in the axils of which sporangia are borne. The American cone specimens consist of a broad axis (or the space once occupied by the axis), about one third the width of the cone, largely hidden by the spirally arranged sporangia. As is often the case in the related genus *Lepidostrobus*, cones of *Polysporia* evidently broke up rather readily into short sections, and neither the base nor the apex of the cone is visible in any of the specimens. The sporophyll lamina is missing from the sporophylls in all the American specimens examined. Only the specimen from Yorkshire (Chaloner, l.c., pl. 2, fig. 1) shows the remains of the distal part of the sporophyll, attached to the pedicel on which the sporangium is borne. It is of course possible that the distal part of the sporophyll was shed in the living plant. However, it seems more reasonable to suppose that as in so many specimens of *Lepidostrobus*, the sporophyll lamina became detached during fossilisation. The sporangia were evidently packed closely together, their outer exposed faces developing polygonal outlines as a result. This is particularly clear in the case of the microsporangia (pl. I, fig. 7). In each of the cones there is a clear demarcation between the megasporangia (in which the megaspores are clearly visible) at one end of the cone, and the microsporangia at the other. By analogy with hermaphrodite *Lepidostrobus* cones, the microsporangiate end is assumed to be distal, and the specimen of pl. 31, fig. 7 is accordingly oriented with this end uppermost.

The spore contents of the cones were investigated by removing fragments of the compressed sporangia, macerating them for twenty-four hours in Schulze's solution (con-

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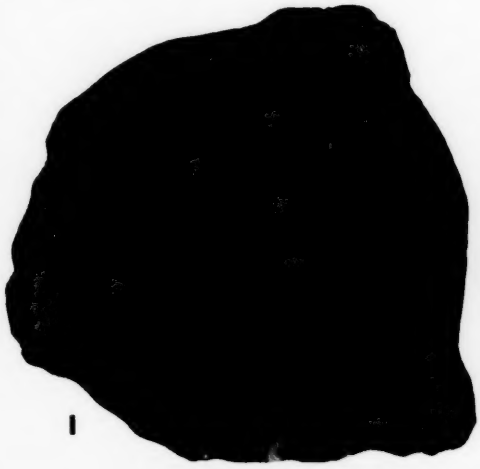
EXPLANATION OF PLATE 31

FIGS. *1–7*—*Polysporia mirabilis* Newberry emend., and its megaspores. *1,2*, megaspores from one of the syntype specimens of *Lepidophyllum truncatum* Lesq. 1879 (the original of his pl. 69, fig. 9, an isolated sporangium from Mazon Creek, Illinois); *1*, by reflected light, and *2*, by transmitted light, ×50. *3*, megaspore from an isolated megasporangium from Mazon Creek, Illinois; by transmitted light, ×50. *4*, megaspore from the holotype of "*Lepidostrobus* (*Macrocystis*) *truncatus*" Lesq. 1884, a cone from Cannelton, Pennsylvania; by transmitted light, ×50. *5*, megaspore from the lectotype of *Polysporia mirabilis* (see fig. 7 below); by transmitted light, ×50. *6*, megaspore from the holotype of "*Lepidostrobus zea*" Chaloner 1953, a cone from Yorkshire, England; by transmitted light, ×50. *7*, the lectotype of *Polysporia mirabilis* Newberry 1873 (the specimen figured in his pl. 41, fig. 6), from Summit County, Ohio; microsporangia above, megasporangia below; megaspores can be seen in large numbers all around the lower part of the cone, and have presumably come from it, ×1. Numbers and locations of the specimens: *1,2,4,5*, U. S. National Museum, Washington, D. C., slides nos. 26051b, 26051a, 16132a and 40925 respectively; *3*, Illinois State Museum, Springfield, Illinois, no. 15742*b*; *6*, Kidston Collection, Geological Survey and Museum, London, England, no. 4838r; *7*, New York Botanic Garden, no. 8449.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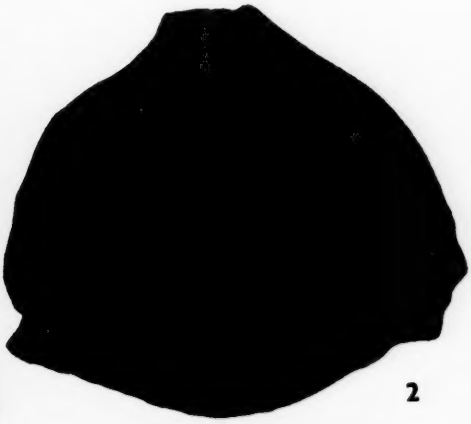
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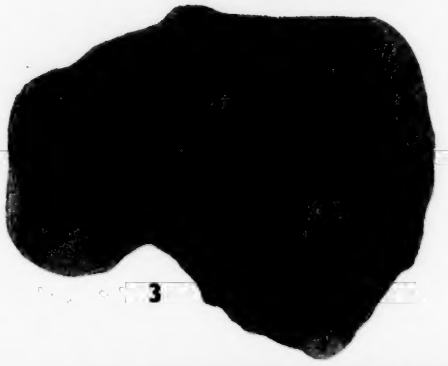
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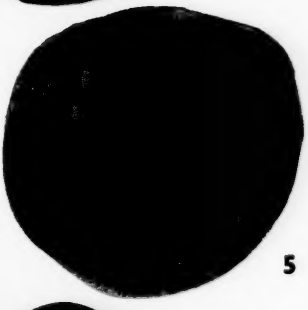
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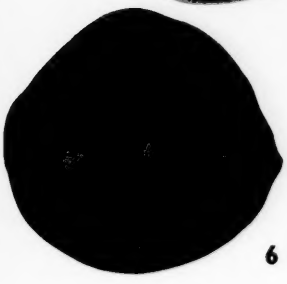
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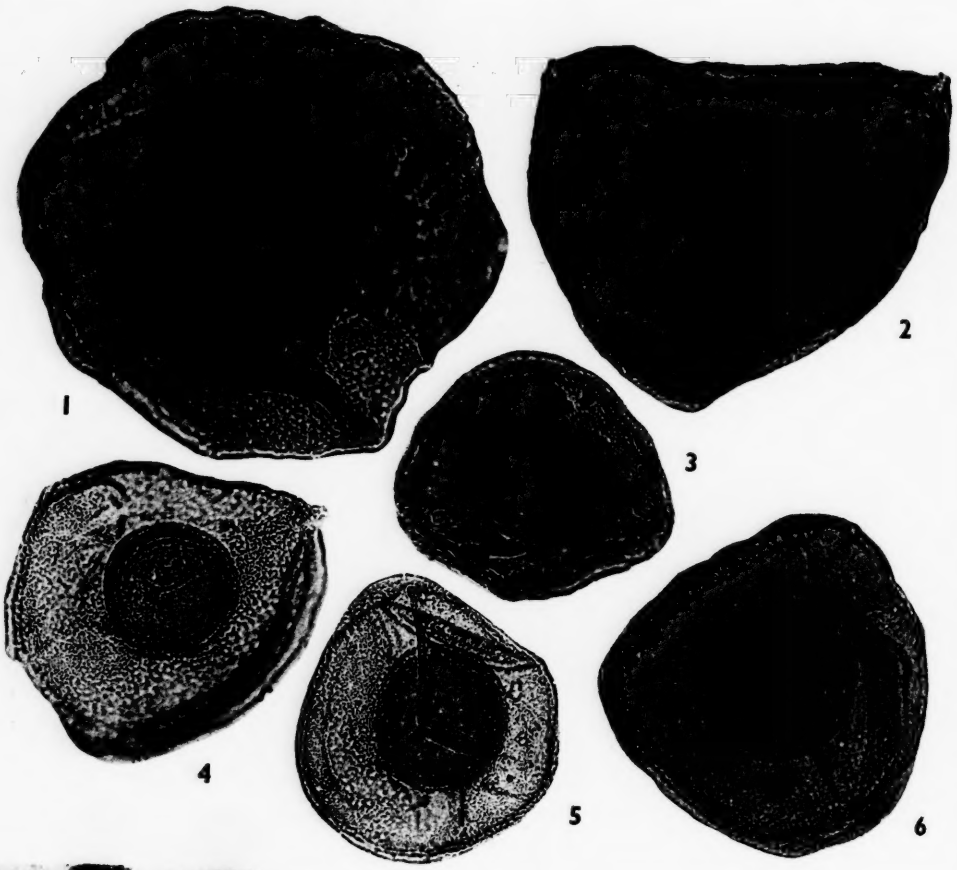
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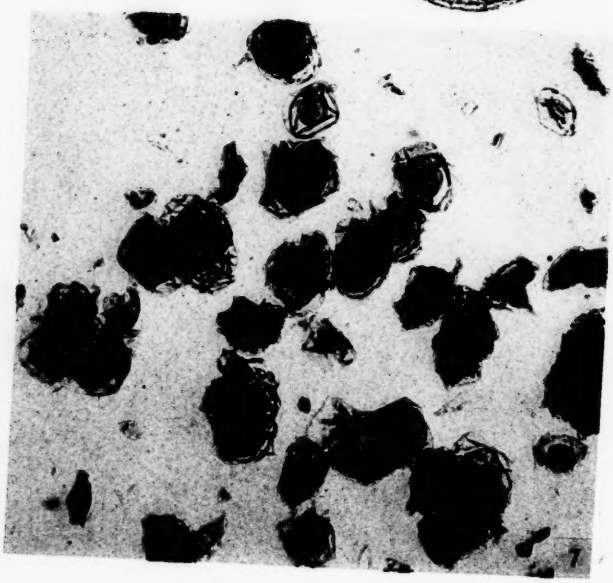
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8

centrated nitric acid and potassium chlorate) and then treating them with dilute ammonia solution. The microsporangial fragments disintegrated into a mass of microspores which were mounted in glycerine jelly (pl. 32). Some of the megaspores were mounted as transparent objects in Canada balsam (pl. 31, fig. 2) and others were examined dry as opaque objects (pl. 31, fig. 1). Whenever possible, at least a hundred microspores from each specimen were examined in detail and measured; in most cases a far greater number of microspores was released on maceration than was actually counted and studied.

For the reasons cited below under "Comparison of *Polysporia* . . . " it is now considered that these cones represent a genus distinct from both *Lepidostrobus* and *Sigillariostrobus*, and Newberry's genus *Polysporia* and the species *P. mirabilis* are emended to include the material described here.

POLYSPORIA Newberry 1873

Synonyms.—See specific diagnosis.

Generic diagnosis.—Large lycopod cones, formed of an axis occupying about one-third to one-half the cone diameter, bearing spirally arranged sporangia in the axils of, or close to the bases of the sporophylls, which have a very readily-shed lamina. Megasporangia in the basal (proximal) part of the cone, containing many auriculate megaspores agreeing with the megaspore-genus *Valvisporites* Ibrahim emend. Potonié & Kremp 1954. Microsporangia in the apical (distal) part of the cone, containing monosaccate microspores, agreeing with the microspore-genus *Endosporites* Wilson & Coe.

The genus is monotypic, *Polysporia mirabilis* Newberry being the genotype.

POLYSPORIA MIRABILIS Newberry 1873 emend.
Pls. 31 and 32

1873. *Polysporia mirabilis* Newberry, p. 362, pl. 41, figs. 5,5a and 6. (The specimen of Newberry's fig. 6 is figured here on pl. 31, fig. 7. This cone has yielded megaspores, see pl. 31, fig. 5, and microspores, see pl. 32, fig. 3).
1879. *Lepidophyllum truncatum* Lesquereux, p. 458, and pl. 69, figs. 9 and 10. (The specimen of Lesquereux's fig. 9 is a megasporangium, spores from which are figured on pl. 31, figs. 1 and 2; the specimen of his fig. 10 is a microsporangium, a spore from which is shown on pl. 32, fig. 1.)
1880. *Lepidostrobus* (*Macrocystis*) *mirabilis* (Newberry) Lesquereux, p. 446. (A re-assignation of Newberry's species.)
1884. *Lepidostrobus* (*Macrocystis*) *truncatus* Lesquereux, p. 784, pl. 108, fig. 1. (A large cone segment which has yielded megaspores, see pl. 31, fig. 4, and microspores, see pl. 32, fig. 8.)
1897. *Sigillariostrobus* Kidston, pl. 2, figs. 1a and b. (Megaspores and microspores from this cone are figured in Chaloner 1953a, pl. 2, fig. 3 and text-figs. 3d,e,g and h.)
1897. "Sporangium" Kidston, pl. 2, figs. 12a and b. (Megaspores were obtained from this specimen: Chaloner, l.c., p. 102.)
1953. *Lepidostrobus zea* Chaloner, p. 97, text-fig. 1, pl. 2, fig. 1. (A large cone segment which has yielded megaspores and microspores, figured here on pl. 31, fig. 6 and pl. 32, fig. 2.)
1954. *Sigillariostrobus? zea* (Chaloner) Potonié, p. 111. (A re-assignation of *L. zea*.)

EXPLANATION OF PLATE 32

FIGS. *1–8*—*Polysporia mirabilis* Newberry emend. Microspores. *1*, from one of the syntype specimens of "*Lepidophyllum truncatum*" Lesq. 1879 (the original of his pl. 69, fig. 10, an isolated sporangium from Cannelton, Pennsylvania), ×500. *2*, from the holotype of "*Lepidostrobus zea*" Chaloner 1953, a cone from Yorkshire, England, ×500. *2*, from the lectotype of *Polysporia mirabilis* (see pl. 31, fig. 7). *4–6*, from a microsporandium from Mazon Creek, Illinois, showing the range in relative size of the air-sac and spore body in spores from a single sporangium; the ratio of spore body diameter to air-sac diameter is 40%, 46% and 50% in these three spores respectively; ×500. *7*, from the same sporangium, showing the spores aggregated in tetrads, ×100. *8*, from the holotype of "*Lepidostrobus* (*Macrocystis*) *truncatus*" Lesq. 1884, a cone from Cannelton, Pennsylvania, ×200. Numbers and locations of the specimens: *1,3,8;* U. S. National Museum, slides nos. 15985a, 40926 and 16132b; *2*, Kidston Collection, Geological Survey & Museum, London, England, no. 4838i; *4,5*, Amt für Bodenforschung, Krefeld, Germany. *6,7*, Illinois State Museum, Springfield, Ill., nos. 15743b and a.

Lepidostrobus truncatus Lesquereux 1870, p. 442, pl. 31, fig. 5, is evidently distinct from the fossil he subsequently described in 1879 as *Lepidophyllum truncatum*, and is not a synonym of *Polysporia mirabilis* (see p. 207 below).

Emended specific diagnosis..—Cone cylindrical, up to 7 cm. in diameter and over 7 cm. in length. Sporophylls composed of a short horizontal part attached to the axis, and passing distally into a relatively long narrow ascending sporophyll lamina, up to 3 cm. long and 8 mm. wide. Sporangia mounted on the upper surface of the sporophyll (or in an axillary position ?) typically about 1.3 cm. long (exceptionally up to 3 cm.), measured perpendicular to the cone axis; typically about 7 mm. in height and breadth (exceptionally up to 15 mm.) measured parallel and tangential to the cone axis respectively. Sporangia having a flattened exposed distal surface, with a pentagonal or hexagonal outline.

Megaspores borne in the lower sporangia of the cone, agreeing with *Valvisporites auritus* (Zerndt) P. & K. 1956. Flattened spore circular, but with three more or less semi-circular flaps extending from the spore equator at the ends of the tri-radiate ridges. Greatest diameter of the flattened spore (from the apex of one semi-circular flap to the opposite point on the margin of the spore body) 520–1360 μ, mean value 833 μ for 173 spores measured (from seven specimens). Tri-radiate ridges up to 50 μ high, reaching to about $\frac{2}{3}$ of the spore radius, with a small expansion formed at their point of confluence. Megasporangia containing several hundred spores.

Microspores borne in the upper sporangia of the cone, agreeing with *Endosporites* Wilson and Coe. Microspore monosaccate, with central spore body originally spheroidal, enclosed in an inflated air-sac, foreshortened in its polar axis, and having a slightly thickened equatorial rim (gula) where the rather flattened proximal face meets the more rounded distal surface of the air-sac. Air-sac attached to the spore body on the proximal face, but free from and passing close to it, on the distal face. Greatest diameter of the flattened spore body 30–66 μ, mean value 47 μ; and of the overall diameter, 66–175 μ, mean value 101 μ; ratio of spore body to overall diameter of air-sac ranging from 33%–72%, mean value 46% (all from measurements of 399 spores from five specimens). Tri-radiate ridges extending to the margin of the spore body, with folds sometimes extending from them onto the surrounding air-sac beyond the area of contact between it and the spore body. Interradial papillae sometimes evident between the tri-radiate ridges near the apex, on the spore body. Wall of air-sac micropunctate to microreticulate; that of the central body undecorated.

Lectotype (pl. 31, fig. 7).—No. 8449 in the New York Botanic Garden collection (figured by Newberry 1873, pl. 41, fig. 6). From the roof of the No. 1 Coal, Tallmadge, Summit County, Ohio; this is of Sharon age, according to Dr. J. M. Schopf (*in litt.*, Sept. 1954), and so approximately equivalent to the Westphalian A of the European sequence (Moore et al., 1944). Newberry (1873) figured two specimens (pl. 41, figs. 5 and 6); only the original of his fig. 6 has been examined, and this has been designated the lectotype. The original of his fig. 5 has not been examined, but this is regarded as a syntype.

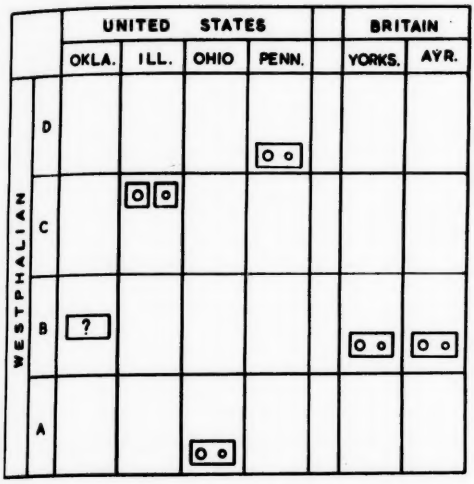
Range and distribution.—From the Westphalian A to C (or ?D), Pennsylvanian. From Illinois, Ohio and Pennsylvania, U.S.A.; and from Yorkshire, England and Ayrshire, Scotland. This information is tabulated in text-fig. 1. Fuller details of the specimens are given below.

SOURCES OF MATERIAL

In addition to the lectotype, the following specimens have been examined, and are regarded as belonging to this species. They are listed under the localities from which they were collected; their present location and Museum catalogue number is also given.

Illinois.—No. 26051, U. S. National Museum, Washington D.C. A megasporangium from a Mazon Creek nodule, Illinois (equivalent to the Westphalian C of the European sequence, from the correlation chart of Moore et al., 1944). One of the two specimens of *Lepidophyllum truncatum* Lesquereux 1879 figured by that author (pl. 6, fig. 9). Megaspores obtained from this specimen are shown on pl. 31, figs. 1,2.

Nos. 15742 and 15743, Illinois State



TEXT-FIG. 1—Diagram showing the distribution of *Polysporia mirabilis*. The symbols represen detached megasporangia (large circle in square), microsporangia (small circle in square) and whole cones containing both megaspores and microspores (two circles in rectangle). The queried record of a cone from Oklahoma is referred to in the text on this page. The horizons are given with reference to the European Westphalian sequence, from the correlation table of Moore et al., 1944.

Museum, Springfield, Illinois. Groups of megasporangia and microsporangia respectively, both compressions in Mazon Creek nodules. Spores from these specimens are shown on pl. 31, fig. 3 and pl. 32, figs. 4–6.

Pennsylvania.—No. 15985, U. S. National Museum, Washington D. C. A microsporangium from Cannelton, Pennsylvania; the second of the two specimens of *Lepidophyllum truncatum* Lesq. 1879 figured by that author (his pl. 69, fig. 10). The age of this specimen is that of the Upper Kittaning Coal (White, 1900, p. 150) and hence Westphalian C or D (correlation chart of Moore et al., 1944). A microspore from this microsporangium is shown on pl. 32, fig. 1.

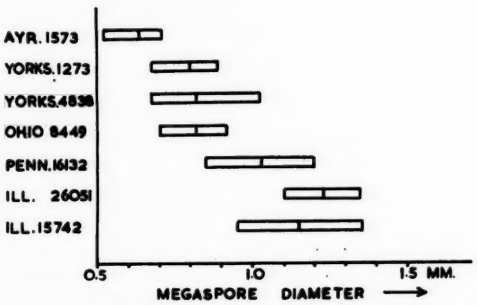
It may be seen from this that Lesquereux founded his species *Lepidophyllum truncatum* on two specimens: one a megasporangium from Illinois, the other this microsporangium from Pennsylvania. This is perhaps the more remarkable since he evidently did not make spore preparations from either.

No. 16132, U. S. National Museum, Washington D.C. The holotype of *Lepidostrobus* (*Macrocystis*) *truncatus* Lesq. 1884; also from Cannelton, Pennsylvania (Westphalian C or D). Spores from this cone are shown on pl. 31, fig. 4 and pl. 32, fig. 8.

Oklahoma.—Dr. D. White (1899, p. 532) identified a specimen from Oklahoma as *Lepidostrobus* (*Macrocystis*) *truncatus* Lesq. This was recorded from the "Roof of the Grady Coal, 2 miles East of Krebs, Oklahoma." Dr. J. M. Schopf (in litt., Sept. 1954) has suggested that this locality implies an Upper Pottsville (i.e. Westphalian B) age. I have been unable to locate Dr. White's specimen, and I am therefore unable to assign it with certainty to *P. mirabilis*. I have marked this record with a query in the table of text-fig. 1.

DISCUSSION

Megasporangia and megaspores.—Megaspores were obtained from four cones and some detached sporangia as enumerated above. The size-ranges of the megaspores and their mean diameters are shown in text-fig. 2. Some of the detached megasporangia are rather larger than those in the assembled cones (viz., up to 1.4 cm. wide, as against 1.0 cm. in the cones). I do not consider this as very significant in view of the overlap in size range of the megaspores from both



TEXT-FIG. 2—Diagram showing the range in size of the megaspores obtained from seven specimens of *Polysporia mirabilis*. The rectangular strips indicate the range of size shown by the spore population of each specimen; their mean value is indicated by the vertical mark near the center of each strip. The source of the specimens is given at the left-hand margin, followed by the catalog number of the specimen, which is quoted in the text. The results are plotted from measurements of 8, 29, 61, 62, 3, 4 and 6 megaspores from each of the seven specimens respectively.

isolated sporangia and cones (cf. text-fig. 2).

It is interesting to compare the ranges in size and structure of the megaspores obtained from *Polysporia* with those of the megaspore-species to which dispersed spores of this general type have been referred. Dijkstra (1946) recognizes only one species of auriculate megaspore showing a close similarity to the megaspores of *P. mirabilis*, namely *Triletes auritus*. Within this species he recognizes a *var. grandis*, differing from the species only in its larger size. It is significant that the spores of *Polysporia mirabilis* range across the size demarcation between *T. auritus* and the *var. grandis* as recognized by Dijkstra.

Pontonié & Kremp (1956) take a narrower generic and specific interpretation than Dijkstra; they place all auriculate megaspores in a separate genus, *Valvisporites*, within which they recognize several distinct species which Dijkstra has "lumped" under *T. auritus*. Those bearing an obvious similarity to the megaspores of *Polysporia mirabilis* are *Valvisporites auritus*, *V. flavus* and *V. augustae*. It would seem that the megaspores from a single cone could be assigned in some cases to more than one of these species (e.g., the megaspores from the Illinois megasporangia of *P. mirabilis* range across the 1100μ size demarcation which Potonié & Kremp regard as the maximum for *V. auritus* and the minimum for *V. flavus*, and show a general similarity to both these types).

It therefore appears that the species of isolated megaspore which corresponds most closely with the megaspores of *P. mirabilis* is *Triletes* (*Valvisporites*) *auritus*, s.l., as interpreted by Dijkstra 1946.

The fact that the megaspores from this cone species range in form through groups recognized as distinct "species" in populations of dispersed spores does not invalidate those species. Dispersed megaspores are fossils of a different category from spore-bearing cones, and the limits of the species must be decided on different grounds, including their stratigraphic ranges. However, the evidence from *Polysporia* suggests that Dijkstra's broad specific interpretation may be more justified than the larger number of species recognized by Potonié & Kremp.

Pontonié's recognition of all Carboniferous auriculate megaspores as a distinct genus, *Valvisporites*, seems useful, as spores of this type are now known to correspond with a distinct type of parent cone, *Polysporia*, differing in several important features from typical *Lepidostrobus* and *Sigillariostrobus*.

Microsporangia and microspores.—When any small spores are obtained from a compression fossil by maceration, there is always some possibility that extraneous (foreign) small spores may have found their way into or onto the fossil either by drifting on the wind onto the living plant or by being washed into it during fossilisation. The author has previously urged (1953b) that any worker claiming a correlation between small spores and their fructification, based on maceration of compression fossils, should state fully the evidence for its validity. Because of the contamination risk just mentioned, a direct relationship between spore and parent plant cannot be automatically concluded on what amounts merely to close association. If a mass of compressed spore exines representing the "mummified" contents of an undehisced sporangium yields a large number of a single type of microspore on maceration, this obviously represents very convincing evidence that the spores are present in their original fructification. But in general, evidence from maceration of compressions (particularly if anything less than say a hundred spores are obtained) is much less satisfactory than a case in which spores are found inside unbroken sporangium walls in petrified material. However, even with compression fossils, the repeated occurrence of a spore in a particular fructification at several localities gives a much greater degree of certainty to their correlation.

Endosporites was believed to be a genus of Cordaitalean pollen until it was found in cones of *Polysporia* (Chaloner 1953a). The four microspore-bearing specimens of *Polysporia mirabilis* from three widely separated localities in the United States confirm that the spore genus *Endosporites* includes (at least in part) lycopod microspores.

As with the megasporangia, some of the isolated microsporangia were markedly bigger (e.g., those from Illinois, up to 1.5 cm. wide and 3.0 cm. long) than those seen

assembled in cones (typically 1.0 cm. wide and 2.0 cm. long). The size range of the microspores from the detached sporangia is quite comparable with that of the spores from the cones (cf. the 2nd and 4th histograms in text-fig. 3 from isolated sporangia, compared with the remainder, from cones). There is therefore no convincing evidence that these larger microsporangia represent a distinct species.

The structure of the microspores of *P. mirabilis* has already been discussed (Chaloner, l.c.). Apart from the increase in size range, the spores in the new American material add little to this. The microspores clearly correspond with those dispersed spores included in the genus *Endosporites*. Pontonié (1952) demonstrated that spores of this type have an enclosing air-sac, attached to the spore body on the proximal face, but free from it on the distal face. The air-sac is micropunctate to microreticulate, and the spore body undecorated. The microspores sometimes show three small dark spots (interradial papillae) between the triradiate ridges, near the spore apex (pl. 32, fig. 2). These are apparently thickenings of the spore body itself, since they show most clearly when the air-sac is poorly preserved or missing. This feature was first observed in *Endosporites* by Kosanke (1950, p. 36).

Pontonié & Kremp (1956) recognize three species of *Endosporites* which are clearly similar to the microspores of *P. mirabilis;* they emphasize the diagnostic importance of the width of the flattened air-sac (saccus of those authors) in relation to the size of the spore body. Typical figures for this ratio of the spore body diameter to the overall diameter of the air-sac for the three species (expressed as a percentage) are:

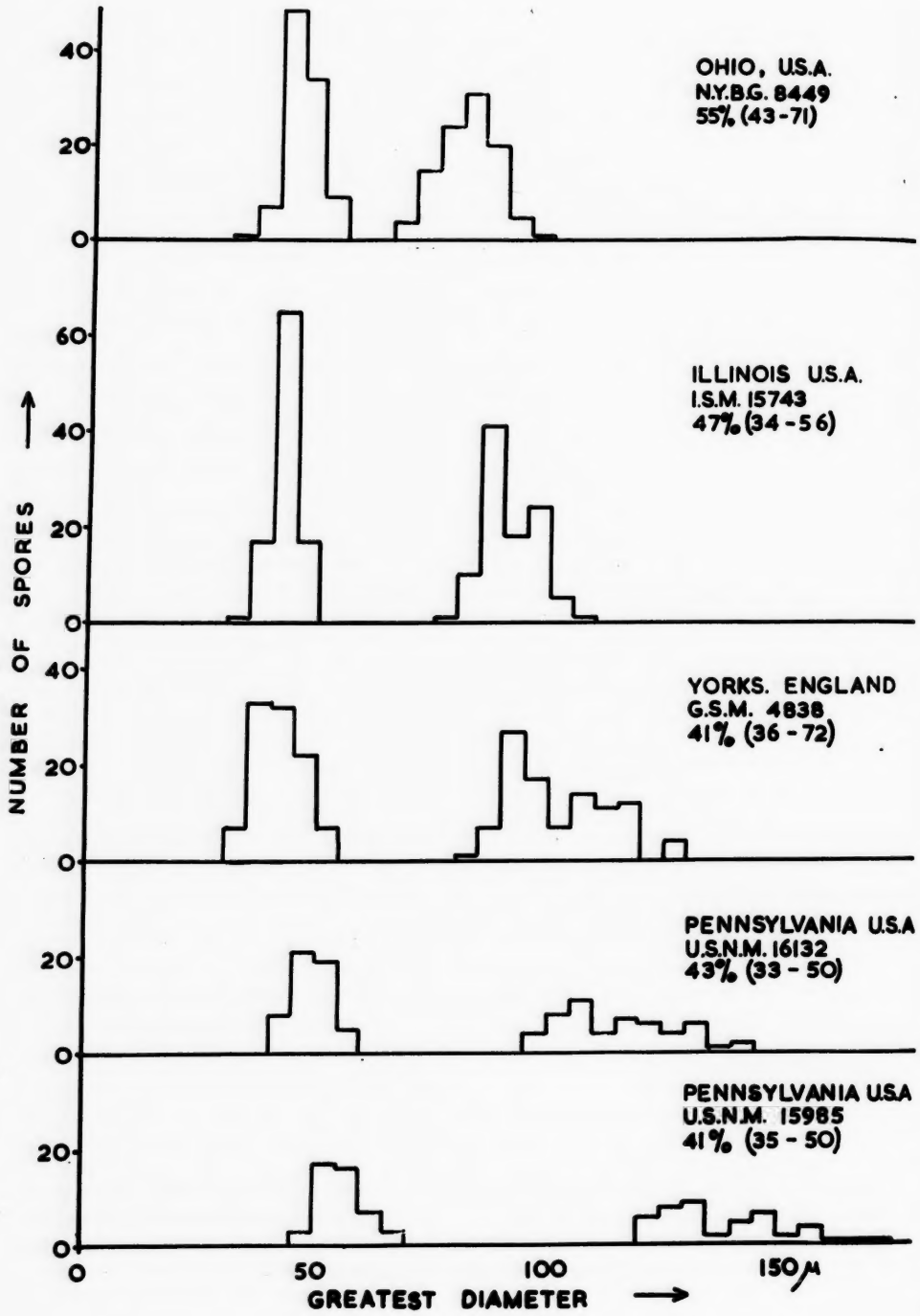
Endosporites globiformis 38%
E. ornatus 48%
E. zonalis 68%

(This is based on the data given by Potonié & Kremp, l.c.; they actually cite the ratio of the body radius to the width of the flattened saccate margin. I have adjusted their figures accordingly.)

Text-fig. 3 shows the dimensions of the spore body and air-sac for five specimens of *P. mirabilis*. Beside each histogram the mean percentage value of the ratio of the spore body to air-sac diameter, and the range of this value, are quoted. It can be seen from these figures that microspores from the *P. mirabilis* cone from Yorkshire show a ratio ranging through the values cited by Potonié & Kremp for these three species of *Endosporites*. Even the microspores from a single sporangium (cf. pl. 32, figs. 4–6) range between *E. globiformis* and *E. ornatus, sensu* Pontonié & Kremp (the three spores figured having a spore body—air-sac ratio of 40%, 46% and 50% respectively). It appears from this evidence that the specific limits taken by these authors may be narrower than those which can be consistently and satisfactorily recognized as a single species of parent cone. However, as with the megaspores, it may be convenient to recognize subdivisions of this nature in the dispersed spores for stratigraphic purposes.

Affinities of Carboniferous monosaccate spores and pollens.—Three kinds of Carboniferous monosaccate spores have now been related to their parent plants. There is the microspore of the lycopod *Spencerites* (agreeing with the dispersed spore *Microsporites* Dijkstra, in part—*Spencerisporites* Chaloner) in which the air-sac is attached to the spore body both proximally (i.e. near to the triradiate mark) and distally. There is the microspore of *Polysporia* (agreeing with the dispersed spore *Endosporites*) where it is attached on the proximal side only. Finally, there is the pollen of *Cordaites* and *Lebachia* (agreeing with the dispersed spore *Florinites*) in which it is attached on the distal side only. In addition, Remy (1954a,b) has found monosaccate spores in some Pteridosperm fructifications, but the details of the attachment of the air-sac are not yet known for all his types. Remy discusses the affinities of monosaccate spores at some length, and reaches rather different conclusions from those expressed here.

Polysporia mirabilis *a single species.*—Although the specimens described here come from widely separated localities, and there is some difference in age, they are identified as a single species because of the agreement in gross morphology and the structure of their megaspores and microspores. There is some difference in the size of the megaspores from the various specimens, but this occurs within the American specimens, and does not offer


OHIO, U.S.A.
N.Y.B.G. 8449
55% (43-71)
ILLINOIS U.S.A.
I.S.M. 15743
47% (34-56)
YORKS. ENGLAND
G.S.M. 4838
41% (36-72)
PENNSYLVANIA U.S.A
U.S.N.M. 16132
43% (33-50)
PENNSYLVANIA U.S.A
U.S.N.M. 15985
41% (35-50)
NUMBER OF SPORES
0
20
40
60
50
100
150μ
GREATEST DIAMETER

a basis for separating the European from the American material. It may be that the older specimens have slightly smaller megaspores than the younger, but there is not sufficient data to show this as a significant difference. In any case there is a large degree of overlap between all the megaspore populations. Many dispersed spores have quite long ranges and are of widespread occurrence within the Pennsylvanian of America and Europe. It is therefore not surprising that a single species of spore-bearing cone should prove to have a comparable distribution in time and space.

Lesquereux's taxonomy.—Lesquereux distinguished "*Lepidostrobus*," "*Lepidophyllum*" and "*Lepidostrobus* (*Macrocystis*)" as entirely different genera; he accordingly used *Lepidostrobus truncatus* Lesq. 1870 (a cone), *Lepidophyllum truncatum* Lesq. 1879 (a sporangium) and *Lepidostrobus* (*Macrocystis*) *truncatus* Lesq. 1884 (a cone) as three separate binomials, basing each on a separate type specimen. The last two prove to be synonyms of *Polysporia mirabilis;* but the first specimen is distinct, and Lesquereux later assigned this cone (*Lepidostrobus truncatus* Lesq. 1870) to his own species, *Lepidostrobus connivens* Lesq.

Other authors (e.g., Scott 1909) have used binomials differently, e.g., *Lepidostrobus veltheimianus* for the cone believed to have been borne on the stem type *Lepidodendron veltheimianum*, both being presumably based on a single type specimen.

The genus Gymnostrobus *Bureau.*—Pant (1956) recently cited Lesquereux's *Lepidophyllum truncatum* Lesq. 1879 as a stigmarian xylem core, together with various other specimens placed by Bureau (1914) in the genus *Gymnostrobus.* In the case of this specimen, however, he was mistaken. *Lepidophyllum truncatum* Lesq. is a specimen of *Polysporia mirabilis*, a lycopod cone, and spores have been obtained from the syntype specimens. With this exception, Pant's general conclusions on *Gymnostrobus* are doubtless valid.

COMPARISON OF *Polysporia* WITH OTHER CARBONIFEROUS LYCOPOD CONES

In first describing the two British specimens here assigned to *Polysporia mirabilis*, the author named them *Lepidostrobus zea* (Chaloner 1953a), using *Lepidostrobus* in a broad sense. Potonié (1954, p. 110) queries this procedure, and suggests the combination "*Sigillariostrobus? zea* (Chaloner) Potonié." The plant which bore these cones is still unknown; however, the spores show important differences from those of typical *Sigillariostrobus* and *Lepidostrobus.* For this reason it is considered desirable to recognize these cones as a distinct genus, the name *Polysporia* being already available.

Table 1 shows the various features which are considered to have diagnostic value in separating the genera of lycopod cones found as compressions. Considerable importance is attached to spore structure in this respect. In those specimens where they are present, the spores are usually the only cutinized structures to survive in a cone compression, and so be available for maceration and subsequent microscopic examination. Spores also have a peculiar significance as one of the few features in which petrifactions and compressions of the same type of cone can be compared in some detail (cf. Schopf 1941b, Chaloner 1953c). It may now fairly be said that the spores obtained from lycopod compressions have proved to be a consistent and valuable guide to generic affinity of the cone.

TEXT-FIG. 3—Histograms of microspore size of populations from five specimens of *Polysporia mirabilis.* The greatest diameter shown by the flattened spore body, and that of the encircling air-sac was measured for each spore. The spore body diameter produces the "population" on the left of each diagram, and the larger air-sac that on the right. The histograms are plotted from 100 spores measured from each specimen, except for the last two which are based on 53 and 46 spores respectively.

The mean value of the ratio "diameter of spore body/diameter of air-sac" (expressed as a percentage) is given for each specimen. The figures in brackets are the ranges of values in each case.

The source of each specimen is indicated; the initials and numbers refer to the collections in which the specimens are housed, and by which they are referred to in the text.

TABLE 1.—COMPARISON OF SIX GENERA OF LYCOPOD CONES

Cone	*Polysporia*	*Sigillariostrobus*	*Lepidostrobus*	*Sporangiostrobus*	*Lepidocarpon*	*Selaginellites*
Parent Plant:	?	*Sigillaria*	*Lepidodendron*	?	? *Lepidophloios*	*Selaginellites*
How borne on parent plant:	?	On a specialized peduncle borne laterally on the trunk	Apically on undifferentiated leafy shoots	?	? Apically on undifferentiated leafy shoots	Apically on undifferentiated leafy shoots
Ratio of diameter of axis to diameter of cone:	⅓–½	½ or less	½ or less	½ or more	½ or less	½ or less
Shedding of sporophyll or sporophyll lamina:	Sporophyll lamina usually missing, leaving the sporangia attached to the axis	Lamina rarely detached from proximal part, but sporophyll often shed whole	Sporophyll lamina often missing, leaving sporangia on proximal part of sporophyll attached to cone axis	Sporophyll lamina usually missing, leaving sporangia attached to the axis	Entire megasporophyll containing "seed megaspore" detached from axis at maturity	Whole cone usually survives fossilization intact. Isolated sporophylls not reported
Structure of megaspores:	Rounded-triangular smooth-walled, with auriculate flaps opposite the tri-radiate ridges	Circular, triradiate, smooth-walled or apiculate, originally concavo-convex	Circular, triradiate, smooth-walled or spinose, contact faces expanded to form an apical prominence	Circular, tri-radiate broad equatorial flange formed of outgrowths of spore wall	One large, elongate "seed-megaspore" per tetrad; the other three small, abortive	Rounded-triangular, triradiate; narrow, continuous equatorial flange merging into spore wall, or absent
Genera to which dispersed megaspores have been referred:	*Valvisporites* (Auriculati section of *Triletes*)	*Laevigatisporites*, *Tuberculatisporites* (Mazospora section of *Triletes*)	*Lagenicula*, *Lagenoisporites* (Lagenicula section of *Triletes*)	*Superbisporites*. (Zonales section of *Triletes*)	*Cystosporites*	*Triangulatisporites*, *Bentsisporites* (Triangulati section of *Triletes*)
Structure of microspores:	Rounded-triangular triradiate, monosaccate; air-sac attached to body on proximal face only	More or less circular, triradiate, smooth-walled, punctate or spinose, without flange or air-sac	More or less circular, triradiate, smooth-walled or punctate with a marginal flange	?	More or less circular, tri-radiate, with a marginal flange	More or less circular, triradiate, with marginal thickening and flange, and thin walled distal area
Genera to which dispersed microspores have been referred:	*Endosporites*	?*Planisporites*	*Lycospora* and ?*Planisporites*	?	*Lycospora*	*Cirratriradites*
Arrangement of megasporangia and microsporangia:	Cones hermaphroditic, megasporangia proximal, microsporangia distal	Cones unisexual	Cones unisexual or hermaphroditic; if the latter, megasporangia usually proximal, microsporangia distal	Cones unisexual, but doubtfully hermaphroditic specimens reported	Cones unisexual	Cones hermaphroditic

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VIVIPAROUS *TURRITELLA PILSBRYI* GARDNER

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ABSTRACT—A second example of *Turritella pilsbryi* Gardner, Yorktown Miocene, of York River, Yorktown, Virginia, containing embryonic shells was discovered. One hundred and four juveniles of the species were within the body cavity, confirming the original suggestion that the species was viviparous. The associated Foraminifera were identified. Attention is called to a former discovery of an individual of each of two species of viviparous fossil Turritellas.

INTRODUCTION

AN INTERESTING specimen of *Turritella pilsbryi* Gardner and its brood of juveniles which had been in the sand within the adult shell when discovered were recently presented to me by Corinne and George Barclay of Newport News, Virginia. The Barclays collected the specimens from the Yorktown Miocene, on the York River, 9 miles north of Yorktown, Virginia. The author is indebted to the Barclays and extends appreciation for the gift of the fossils.

After the shell had been received, 104 embryonic individuals were counted. This represented probably a small portion of the original lot.

Dr. Julia Gardner (1948, p. 196, pl. 27, figs. 11,25), who described the species, first observed the above phenomenon when she cleaned one of her large shells. She did not state how many adults were available but did not that Wendell P. Mansfield reported the species from a number of Yorktown Miocene localities in Virginia, Zone I of the Yorktown formation. The material of the species which I have identified consists of two specimens from the Barclays and five individuals collected by a geology class of Princeton University, locality 199-C, near Yorktown, Virginia, "near the mouth of the York River." Prof. Erling Dorf stated that the "C" referred to the third of 8 zones which might or might not "correspond to Gardner's Bed C mentioned in her 1943 paper (U.S.G.S. Prof. Paper 199A, p. 10)" (Personal communication, May 29, 1956).

MATRIX AND FORAMINIFERA

The Barclay specimens of *T. pilsbryi* came from the same locality. The individual with the juveniles had a yellow sand matrix and the other specimen of *T. pilsbryi* contained grey sand. James D. McLean, Jr., kindly examined the sand from the two specimens, identified the Foraminifera, and supplied the following notes:

"The 'grey sand' sample from a *Turritella pilsbryi* specimen contained no forams and only one ostracode whose identity is not yet clear. Mineralogically, there seems to be a significant difference in the sands from the two specimens, the 'grey sand' is composed of quartz, glauconite, shell fragments and a very adhesive clay which did not wash off the other minerals even through some rough treatment with water and carbon tetrachloride.

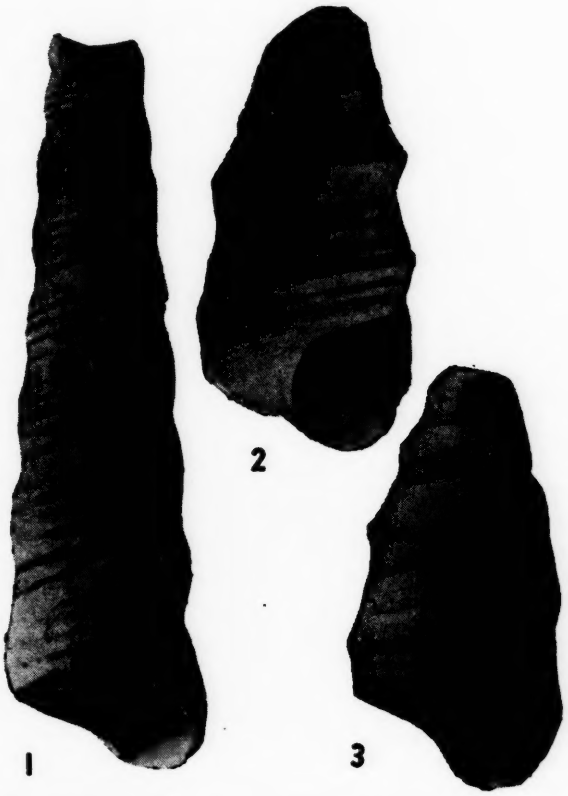
"On the other hand, the 'yellow sand' is composed of quartz, mica flakes, varicolored grains (maybe garnet etc.) and some light-gravity amber-colored clastic grains which could be amber or other resins (perhaps even shellac if the specimen was painted with it). The fauna of this sand is as follows on next page.

"The scarcity of *Sigmomorphina concava* in Yorktownian samples is probably the reason why I have not found it in Zone I so far; on the other hand, *Textularia pseudobliqua* subsp. *aspera* McLean (Bull. Amer. Paleont., v. 36, No. 160) seems to be quite well established as not occurring in the faunas of Zone II, and this form has been found frequently enough in my material and in that of Miss Mongin to establish it as a Zone I guide if older forms do not establish a St. Marys age for a sample. The fauna above is not St. Marys, and so I would say that the 'Yellow sand' from *T. pilsbryi* is Zone I of the Yorktown as far as forams may correlate it."

Pseudopolymorphina rutila (Cushman)..... Zones I & II
Globigerina sp. (Form E)..... Zones I & II
Buccella cf. *parkerae* Andersen..... Zones I & II
Planulina depressa (d'Orbigny)..... Zones I & II
Hanzawaia concentrica (Cushman)..... Zones I & II
Discorbis floridana Cushman..... Zones I & II
Cibicides subloba (Cushman)..... Zones I & II
Cancris sagra (d'Orbigny)..... Zones I & II
Cibicidella variabilis (d'Orbigny)..... Zones I & II
Sigmomorphina concava (Williamson)..... Zone II
Textularia pseudobliqua subsp. *aspera*..... Zone I
Unidentified foraminifer
Ostracode spp.

DISCUSSION

Turritella pilsbryi was well described and figured from the holotype (an adult) and a juvenile (paratype). The form can be determined readily in the large robust adult stage and can be distinguished from associated Miocene Turritellas by the finely executed photograph of the holotype. The full de-



TEXT-FIG. *1*—*Turritella pilsbryi* Gardner; length, 80 mm.; greatest diameter, 24 mm.; Yorktown Miocene, York River, 9 miles north of Yorktown, Va., Paleontological Research Institution, No. 25176.
2—*Turritella pilsbryi* Gardner. Juvenile from shell shown in text-fig. 1; length, 3 mm.; greatest diameter, 1 mm. Paleontological Research Institution, No. 25177.
3—*Turritella pilsbryi* Gardner. Juvenile from shell shown in text-fig. 1; length, 2.5 mm.; greatest diameter 1 mm. Paleontological Research Institution, No. 25178.

scription by Gardner covered details of shell comparison with other species; hence such facts need not be repeated here.

Dr. Garner observed (*op cit.*, p. 196):

"An interesting suggestion of the viviparous habit of the genus is offered in the material on which this species is based. In cleaning one of the larger individuals, a sandy core was shaken out in which 47 embryos were embedded. As they are obviously the larvae of the same species, and as no other shells were present in the core, there seems to be no reasonable doubt that they are the young of the individual which contained them."

The present collection confirms the above discovery and adds a second example of a similar phenomenon. The embryos in the present case were found in a like manner with 104 (plus) embryos embedded in the sandy core of the individual.

The reports of instances of fossil embryos found in place in viviparous species are so rare that it is important that their discoveries be placed on record. Such knowledge is especially of prime value in the study of Turritellas. As the author pointed out in 1937, the literature of fossil Turritellas abounds with names, such as unicarinata, bicarinata, and tricarinata as specific appelations. Such terms have fallen in synonymies and as homonyms have been rejected. They may indicate only stages of development of the shell of the species. (See Palmer, 1937, p. 188; 1947, p. 280; Bowles, 1939, p. 267; Merriam, 1941, p. 5,6.) The initial whorls of Turritellas, Recent and fossil, are difficult to disvover. It is, therefore, of value to find the embryonic shells which correspond to the initial whorls of an individual. In addition, the finding of the embryos in the shell indicates the sex of the fossil as well as the habit. Such facts are impossible to prove in most fossils.

My attention was called by A. A. Olsson to the discovery in 1899 by that expert fossil collector, Frank Burns (1899, p. 68), of two Turritellas containing embryonic shells. Burns discovered at Plum Point, Maryland, Calvert Miocene, a fragment of *Turritella cumberlandia* Conrad (21 mm. × 11 mm.) which contained 200 juveniles. He also found a specimen of *T. indenta* Conrad, same bed at Plum Point, as above, and he stated that the young specimens were in the shell "by the hundreds." The unusual occurrence of such a phenomenon is indicated by Burns' statement: "Of all the great number of thousands of such shells [fossil mollusks] that I have heretofore collected, I never saw anything like this [embryonic shells in mother shell] nor have I read of it."

It is worth comment that four occurrences of viviparous Turritellas noted are from the Chesapeake Miocene, although not from the same formation.

Iredale (1924, p. 247) proposed the generic name *Gazameda* for the Australian *Turritella gunnii* Reeve which included among its distinctive characters a viviparous habit. Peile (1921), as well as Iredale, reported the finding of young within the shell of many specimens of the species.

SUMMARY

1. Occurrence of a second example of adult *Turritella pilsbryi* Gardner, Yorktown Miocene of Virginia, with embryonic young in the body whorl, is placed on record.

2. The phenomenon adds proof that the species is viviparous as originally stated.

3. The features of the embryonic shell indicate the character of the nuclear whorls of the species. This is important in ontogeny of Turritellas, a genus in which the shells of a species have a definite developmental pattern of costation.

4. The identification of the Foraminifera in the sand which was within the shell helps to standardize the mollusks and Foraminifera correlation of the Yorktown Miocene zones.

5. Two examples of viviparous Turritellas were found in 1899 by Frank Burns in the Miocene, Plum Point, Maryland.

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THE DESCRIPTION OF FOSSIL POPULATIONS

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ABSTRACT—Typological contingency tables afford a compromise between standard methods of quantitative analysis of populations and standard methods of their qualitative analysis. Such a compromise combines the advantages of permitting significance tests and assessing confidence limits with those of taking into simultaneous consideration any number of qualitative and quantitative characters. The proposed technique is described and applied to specific cases in Carboniferous corals, Silurian graptolites, and Jurassic oysters.

INTRODUCTION

ALTHOUGH the population concept is not yet universally accepted as the basis of paleontological taxonomy, a recent survey (Sylvester-Bradley, 1956a) suggests that the majority of paleontologists agree that two species concepts exist in the study of fossils—one based on populations, the other on "types." There is considerable disagreement as to which concept is preferable. Many contend that fossils seldom permit deductions on the nature of a population, so that the typological concept is the only practical solution. Others believe that even single specimens are evidence of populations, and that it is essential to base species on populations if paleontology is to contribute its part to the synthesis of evolutionary, ecological, and taxonomic ideas currently discussed by neontologists. Such disagreement, however, is purely semantic, hinging on the definition of the word "species." All agree that populations of exactly the same pattern as exist today also existed in the past. A more fundamental disagreement is apparent in the treatment of such populations. Those who believe in the typological definition of the species commonly describe the extent of variation displayed by giving specific names to "intrapopulation variants" (Mayr, Linsley, & Usinger, 1953, p. 35). Such paleontologists, then, give but a single specific name to a population displaying very little variation, but several specific names to one that was highly variable. The number of names applied to a population thus gives some indication of its variability.

Thus Arkell (1952), in describing a collection of ammonites from Arabia, emphasized the great variation displayed "in one particular stock at one time and place—a range far greater than normal" by assigning them to ten species and three subgenera (Arkell, 1956, p. 99). Mayr (1952, p. 449), commenting on this case, suggested that "all these forms may be no more than individual variants and ecophenotypes of a single species." Mayr was using the term species in the accustomed neontological sense according to the population concept; Arkell was using the category in the typological sense, and was describing the variation shown by the ammonites without speculating on the number of interbreeding groups represented.

Again, thirty-five specimens of rugose coral from a single horizon and locality in the Namurian of Yorkshire were referred by Hudson & Fox (1942, p. 102–103) to five species and three subgenera. These forms were all considered to belong, however, to a single "species-plexus" "composed of forms linked by intermediate varieties." They considered the species-plexus to be, "in a phylogenetic classification, the equivalent of a species."

The distinction between biological species and morphological species is implicit in many paleontological papers, as is self-evident, for example, when Spath (1938, p. 25) states: "The examination of numbers of individuals of *Beaniceras* leads to the conviction that, with the numerous passage-forms to *Androgynoceras* and *Liparoceras*, all the species of *Beaniceras* formed one interbreeding population." He goes on to describe seven "species" of *Beaniceras*, which he regards as generically distinct from both *Liparoceras* and *Androgynoceras*.

On the other hand, invertebrate paleontologists who regard the intrabreeding population as the basic unit of the species are beginning to adopt quantitative methods.

and describe the variation displayed by a population in terms of statistics derived from biometrical data (e.g., Prentice, 1956; Shaw, 1956). Vertebrate paleontologists have for long been using these methods.

In this paper an attempt is made to examine the advantages and disadvantages of both methods when applied by the practicing paleontologist. A compromise is suggested whereby the methods of the qualitative paleontologist can be adapted to the description of populations, and useful statistics can be derived without recourse to the time-consuming rigor of a full-scale biometrical analysis.

BIOMETRICAL ANALYSIS

Imbrie (1956), in his extremely valuable review of biometrical methods used in paleontology, points out that the statistical analysis of quantitative data has three special advantages, which can be restated as follows:

(a) quantitative data are more accurate than qualitative data;
(b) the statistical description of variation can take into account differential growth rates in a way that is impossible by qualitative methods;
(c) statistics supply (1) confidence limits, which show how accurately the variation displayed by a particular collection is a reflection of the variation of the actual population from which it was drawn, and (2) significance tests, which specify precisely what possibility there is of a supposed difference between two or more populations being spurious, and due to chances of sampling.

All paleontologists must agree that a certain amount of quantitative data is essential to the accurate description of specimens. Clearly "25 mm. long" is preferable to "rather long." Most qualitative descriptions of specimens include such data; for example, the description of a species often includes the dimensions and other quantitative data of at least the holotype. It must be evident that, if a population as such is to be described at all, the variation it displays with regard to the holotype is a crucial and important part of its description. If such variation is expressed quantitatively, it is certainly also important to know whether differences observed in the variation of two collections are likely to be due to chance, or to a difference between the populations from which they were drawn. If the difference is statistically significant, it may also be paleontologically significant; if it is not statistically significant, the statistics provide insufficient evidence for any paleontological discrimination.

The advantages of the quantitative approach are therefore considerable. What are the disadvantages? The most cogent hinges on the fact that a fossil is characterized not by one character but by many, and biometrical methods are singularly inefficient at the analysis of more than two characters at a time. The trained paleontologist, viewing a single specimen, can often identify it at once with other specimens known and studied before. As Young (1954, p. 8) has pointed out, the eye and the brain are good at making single comparisons, at coping with one specimen displaying many characters, but are much less good at comparing series of specimens. Biometrical techniques, on the other hand, are good at making comparisons of series of specimens, providing the characters displayed are studied one at a time. Slightly more complicated techniques can deal with two characters at a time. The statistical techniques involving more than two variables become much more complicated (Burma, 1949) and are usually limited to the calculation of discriminant functions—useful only to determine which, of several species that have been statistically analyzed, a particular specimen should be assigned. The method is severely limited, for it breaks down if the specimen does not in fact belong to any of the species that has been analyzed. Moreover, the function itself has no descriptive value, and cannot be translated into paleontological terms. As Imbrie (1956, p. 221) has put it, multivariate analysis is "too laborious and abstract for wide application." The disadvantages of dealing with univariate or bivariate analysis can be clearly demonstrated by considering the question of taxonomic discrimination, dealt with later in this paper (p. 225–227 and 230, 233).

A second argument against quantitative methods is based on the difficulty of choosing quantitative characters that give expression to differences which are paleontologically significant. It is easy to choose for

measurement characters which display variation. Too often it is found that such variation has no paleontological, stratigraphical, or taxonomic significance. The art of the good biometrician is in no small part the art of choosing ingenious measurements which give expression to characters known to be taxonomically significant.

A third formidable argument against the adoption of quantitative techniques is that they are so time-consuming that their employment is virtually impracticable except for the very detailed study of species already well-known qualitatively. It is certainly true to say that many of the papers so far published that have used biometrical statistics for the description of invertebrate fossils have been essays in technique rather than routine paleontology; though there are exceptions (e.g., the recent paper by Prentice, 1956, in which the variation exhibited by three species of brachiopods is quantitatively analyzed during the course of their description) which are perhaps forerunners of a style that may one day become commonplace. Imbrie has argued that "the statistics necessary to characterize the average paleontological sample can be computed in no more time than it takes to prepare a thin section." That may be so; it is not the calculation of the statistics that is mainly responsible for the great increase in time that quantitative methods demand over qualitative methods; it is the preparation of the biometrical data from which the statistics are calculated. In a recent biometrical investigation undertaken by the author on European Bathonian oysters (referred to in more detail later in this paper) it was judged necessary to make nineteen measurements of each specimen in order to assess seven characters. The nature of the investigation demanded the analysis of a large number of samples drawn from a wide geographical area and a number of geological horizons. The average time taken to measure each specimen was about ten minutes. Fatigue, evident after three hours' continuous work, then slowed up the speed considerably. The completion of the work was imperilled by the time it would take to amass the biometrical data. Alternative and less time-consuming means for collecting and generalizing the data were therefore sought, and it is the technique that resulted that is described in this paper.

TYPOLOGICAL ANALYSIS

The traditional method of describing a population by typological analysis has been to divide it into a number of so-called "morphological species," as in the examples cited above (Arkell, 1952; Hudson & Fox, 1942; Spath, 1938). Such species bear no relation to the species as defined by neontologists; they are, in effect, groups of what Mayr, Linsley & Usinger (1953) refer to as "intrapopulation variants." In the deme terminology of Gilmour & Heslop-Harrison (1954), they are "merogamodemes" (Sylvester-Bradley, 1956b)—arbitrarily selected parts of intrabreeding populations. The type-specimens of such "species" are standards of reference to which the population is compared. The population can then be characterized by containing such a proportion of species A, such of species B, such "aff. sp. B" or "aff. sp. A," and such "cf. sp. B" or "cf. sp. A." The system has been successfully employed by British authors working on Coal Measure non-marine lamellibranchs, particularly by Trueman, Weir, Leitch, & Eagar. Belgian workers on the same group of fossils strongly criticize these methods (e.g., Pastiels, 1953), and themselves adopt the fully quantitative approach. Eagar (1956) has defended the method as one that has stood the test of time, and that has succeeded in answering the demands made on it by those interested in the economically important stratigraphy of the Coal Measures. A zonal scheme based on these fossils has long been in general use through Britain, and could presumably be extended through Europe if similar methods were employed.

The particular advantage of the typological method is that it is well understood as it has been the standard method of paleontology for the last 200 years, modified for application to the study of populations. It permits the specialist to name all fossils submitted to him, irrespective of whether they be single specimens derived from a core, or large samples of populations collected in the field. It does not, of course, lead to a more accurate identification of horizon, but the typological approach al-

lows a paleontologist to return a single specimen with a single name, and not an equivocal statement that it may belong to any one of three overlapping subspecies.

A supplementary advantage is the fact that it takes a specialist a much shorter time to divide up a population into morphological species than it does to measure each specimen and work out its biometrical statistics. Finally, the division of a population into morphological species can take into account at one time all characters displayed by the fossils. Biometrical analysis can only deal with those characters amenable to measurement, and can then only conveniently consider them two at a time.

QUANTITATIVE DEFINITION OF MORPHOTYPES

Those paleontologists who believe that the species should be based on the intrabreeding population object to the use of the term "species" to designate arbitrary groups split from a population on the basis of morphology, as in the case of the morphological species considered above. The term "morphotype" (George, 1956) affords a convenient alternative, and it will henceforth be used in this paper.

A morphotype has been defined as "an intrapopulation variant selected to represent the specified morphological peculiarities it displays" (Sylvester-Bradley, 1956a, p. 141). As such it is a single specimen. In this paper the term is used also in a wider sense: "a group of intra-population variants displaying an arbitrarily defined morphological variation." Such a "morphotype-group" is based on a type specimen which might well be described by the first of the two definitions given above.

Some of the disadvantages attendant on the typological analysis of a population can be overcome if the morphotypes are defined in quantitative terms. This applies not only to the description of the type specimen, but also to the limits of variation arbitrarily selected by the particular author. If variation in uncorrelated characters is continuous, such arbitrary limits cannot be drawn unless the population is split up into almost as many morphotypes as there are individuals, or unless some characters are weighted at the expense of others. To adopt the former alternative would be as absurd as to name each specimen individually; but the second, that of weighting certain characters, is an essential part of any paleontological analysis, as distinct from a purely morphological analysis, and renders the technique practical, for all paleontologists are accustomed to select certain characters (which they consider to be more significant) and to overlook others. In the same way morphotypes should be chosen which can be shown to be taxonomically significant by reason of their occurrence in different proportions in populations characteristic of distinct horizons or distinct geographical areas. The problem is dealt with in a particular case below (p. 227–233).

TESTS OF SIGNIFICANCE

If a series of collections ("samples") can be analyzed into morphotypes which, however arbitrary, are yet objectively defined, then it is possible to compare them in tabular form. One of the best known examples of such an analysis was performed long ago by Carruthers (1910) in his study of the Carboniferous coral *Zaphrentites delanouei*. Carruthers divided his collections into four named morphotypes; Hudson (1941) later added two further morphotypes to this series, but, as Carruther's original collections were not available to him, could not give comparative figures of their distribution in collections from the various horizons. Carruthers' results, as condensed previously (Sylvester-Bradley, 1951) are presented in Table 1.

It is possible, using such a table, to apply a simple statistical test of significance which answers the question: "Could such a result have been obtained by chance if there were, in fact, no differences in the constitution of the populations at the four horizons?" Or, in other words: "Could the apparent evolutionary changes demonstrated by Carruthers be spurious, and due only to accidents of collecting? Has Carruthers in fact proved his case or not?"

The method is to treat the tabulated results as a *contingency table*, and apply the χ^2 test of significance to it. It would be possible to do this in one operation, and achieve an immediate answer to the questions asked above, in which case the contingency

TABLE 1.—DISTRIBUTION OF MORPHOTYPES OF *Zaphrentites delanouei* (MILNE-EDWARDS & HAIME) FOUND AT FOUR HORIZONS OF THE CARBONIFEROUS OF SCOTLAND, CONDENSED FROM CARRUTHERS (1910)

Horizon:	*Zaphrentites delanouei;* morphotypes:				Totals
	delanouei	*parallela*	*constricta*	*disjuncta*	
Millstone Grit	0 (0%)	0 (0%)	1 (5.0%)	19 (95.0%)	20
Upper Limestone Group	0 (0%)	1 (0.3%)	51 (16.2%)	263 (83.5%)	315
Lower Limestone Group	5 (0.7%)	22 (3.3%)	474 (69.8%)	178 (26.2%)	679
Cementstone Group	76 (69.1%)	33 (30.0%)	1 (0.9%)	0 (0%)	110
Totals	81	56	527	460	1,124

table would be an $n \times n$ table. Such a method, however, is not so informative as when the results are considered in couples ($2 \times n$ tables), for then one can find out just how much of the material studied is adequate, and how much still needs corroborative evidence before it can be considered "proved." $2 \times n$ tables are usually more satisfactory for typological analysis than are $n \times n$ tables.

In general, the χ^2 test provides a method for determining the probability (P) that observed results (O) are due to chance, and it is necessary first to calculate what the expected results (E) would be if chance were the sole controlling factor. The method is fully described in all statistical texts, and it is only necessary here to remind readers that

$$\chi^2 = \sum \frac{(O-E)^2}{E}.$$

Once having calculated χ^2, it is necessary to know the degrees of freedom present, when P can be read directly from tables. If P is greater than 0.05, it is possible that the results *are* due to chance; they are described as "not significant." If P is less than 0.01, not once in a hundred times could such results occur by chance, and they are described as significant. If P lies between 0.01 and 0.05, the results are probably significant.

When applied to a $2 \times n$ contingency table, there is a convenient short method of calculating χ^2. If the results are tabulated as shown in Table 2,

$$\chi^2 = \frac{\sum g - nG}{G(1-G)}$$

and the degrees of freedom are given by the number of morphotypes, less 1. In Table 2 there are 4 morphotypes, so there are 3 degrees of freedom. There is one stipulation: if the value of the *expected* frequency in any of the cells a, b, c, d, A, B, C, or D is less than 5, the χ^2 test becomes too inexact to be adequate. The expected frequency for a cell is given by:

$$\frac{n(a+A)}{n+N}.$$

If in any table a cell with $E < 5$ occurs, the table must be reconstructed by combining together either two or more vertical columns (i.e., combining together two or more morphotypes), or two or more horizontal columns (combining together two or more collections).

The point is illustrated if we first consider the upper two horizons of Carruthers' data. Abstracting these from Table 1, we get Table 3. The observed frequency in the Mill-

TABLE 2.—2×n TYPOLOGICAL CONTINGENCY TABLE, showing method of derivation of the values g and G for substitution in the formula for the determination of χ^2 given in the text

Collections	Morphotypes				Totals
	α	β	γ	δ	
X Y	a A	b B	c C	d D	n N
Totals	a+A	b+B	c+C	d+D	n+N
g	$\frac{a^2}{a+A}$	$\frac{b^2}{b+B}$	$\frac{c^2}{c+C}$	$\frac{d^2}{d+D}$	Σg
G					$\frac{n}{n+N}$

TABLE 3.—MORPHOTYPES OF *Zaphrentites delanouei*; TYPOLOGICAL CONTINGENCY TABLE FOR THE UPPER TWO HORIZONS ABSTRACTED FROM TABLE 1

Horizons	Morphotypes		Totals
	parallela+*constricta*	*disjuncta*	
Millstone Grit	1	19	20
Upper Limestone Group	52	263	315
Totals	53	282	335

stone Grit of the morphotypes *parallela* and *constricta* being only 1, and the total for the horizon only 20, it is at once apparent that the expected frequency in this cell may fall below 5. The calculation

$$\frac{53}{335}\times 20=3.16$$

quickly shows that this indeed is the case, and that therefore the χ^2 test will not be adequate. As, however, the data have in this case been reduced to a 2×2 table, it is possible to use an exact method for determining the value of P, not dependent on the distribution of χ^2 (Fisher, 1954, §21.02; see p. 220 below). Such a calculation applied to Table 3 shows that $P=0.15$. There is thus insufficient evidence to establish any significant difference between the collections from these two horizons. It is therefore permissible to group them together when comparing them, in the next couple, with the collections from the Lower Limestone Group (Table 4). Once again, it is wise to test whether the expected frequency of the morphotypes *delanouei* and *parallela* in the Millstone Grit and Upper Limestone Group exceeds 5, as the observed frequency is so low, and the total for these morphotypes is only 28:

$$\frac{28\times 335}{1014}=9.25.$$

In this case, then, the expected frequency is high enough to give a valid result, and we can proceed to calculate χ^2 from the table as it stands, using the formula given above, thus:

$$\chi^2=\frac{178.48-110.68}{0.3304\times 0.6696}=306.1.$$

With 2 degrees of freedom, P is much less than 0.001, and the results are highly significant.

Similar calculations can be made for the remaining couple as shown in Table 5, which gives results that are even more highly significant.

Summarizing, then, we can say that Carruthers' figures show that the populations sampled by his collections from the lower three horizons can clearly be distinguished by the proportions of the morphotypes that each carries. Carruthers' material is insufficient, however, to determine whether or not the populations characteristic of the Upper Limestone Group and the Millstone Grit can be distinguished from each other. This conclusion is in conformity with that previously established by other means (Sylvester-Bradley, 1951).

The same general methods apply even when it has only been possible to divide the collections up into two morphotypes. The result is a 2×2 table, with only one degree of freedom. If the data are set out as in Table 6,

$$\chi^2=\frac{(p+q)\ (ad+bc)^2}{pqrs}$$

TABLE 4.—MORPHOTYPES OF *Zaphrentites delanouei*; TYPOLOGICAL CONTINGENCY TABLE FOR THE UPPER THREE HORIZONS, ABSTRACTED FROM TABLE 1

Horizons	Morphotypes			Totals
	delanouei+*parallela*	*constricta*	*disjuncta*	
Millstone Grit+Upper Limestone Group	1	52	282	335
Lower Limestone Group	27	474	178	679
Totals	28	526	460	1014

TABLE 5.—MORPHOTYPES OF *Zaphrentites delanouei*; DERIVATION OF χ^2 FROM TYPOLOGICAL CONTINGENCY TABLE FOR THE LOWER TWO HORIZONS, ABSTRACTED FROM TABLE 1

Horizons	Morphotypes				Totals
	delanouei	*parallela*	*constricta*	*disjuncta*	
Lower Limestone Group	5	22	474	178	679
Cementstone Group	76	33	1	0	110
Totals	81	55	475	178	789
$\chi^2=629$	Degrees of freedom = 3			$P<0.001$	

The χ^2 test is less successful in dealing with 2×2 tables than with $2\times n$ tables, and tends to give results which underestimate the value of P. In marginal cases (say, when P lies between 0.01 and 0.10) it may be advisable to apply "Yates' correction for continuity" (fully explained in statistical textbooks), which, however, has a tendency to overestimate the value of P. An exact method for estimating P for 2×2 tables has been worked out by Fisher (1954, §21.02) and, although more laborious than the χ^2 test, can always be applied to critical cases.

The use of a 2×2 table can be well demonstrated by considering the results published by Challinor (1945), which are summarized in Table 7. In this work Challinor collected a series of graptolites belonging to the three morphological species (morphotypes as here understood) *Monograptus fimbriatus*, *M. raitzhainiensis*, and *M. triangulatus* from 5 successive horizons within the Llandovery (Silurian) of Wales. Each horizon consisted of a bed about one foot in thickness separated from the others by less fossiliferous shale; the whole section measured 25 ft.

TABLE 6.—2×2 TYPOLOGICAL CONTINGENCY TABLE SHOWING METHOD OF DERIVING TERMS FOR SUBSTITUTION IN THE FORMULA FOR DETERMINATION OF χ^2 GIVEN IN THE TEXT

Collections	Morphotypes		Totals
	α	β	
X	a	b	a+b=r
Y	c	d	c+d=s
Totals	a+c=p	b+d=q	p+q=r+s

TABLE 7.—DISTRIBUTION OF MORPHOTYPES OF *Monograptus triangulatus* (HARKNESS) FOUND AT FIVE HORIZONS IN THE SILURIAN OF WALES (AFTER CHALLINOR, 1945)

Horizons	Morphotypes		Totals
	fimbriatus + *raitzhainiensis*	*triangulatus*	
4	40 (77%)	12 (23%)	52
2d	65 (78%)	18 (22%)	83
2c	32 (82%)	7 (18%)	39
2b	34 (94%)	2 (6%)	36
2a	25 (100%)	0 (0%)	25
Totals	196	39	235

Challinor was unable to separate *M. fimbriatus* from *M. raitzhainiensis* with sufficient objectivity to give unprejudiced results, and was thus forced to unite them, leaving only two morphotypes as listed in Table 7. The steady percentage increase of the morphotype *M. triangulatus* suggest a gradual evolutionary change. The significance can be calculated for each pair of horizons in turn. In Table 8 are set out the data for the upper

TABLE 8.—MORPHOTYPES OF *Monograptus triangulatus*; TYPOLOGICAL CONTINGENCY TABLE FOR THE UPPER TWO HORIZONS, ABSTRACTED FROM TABLE 7

Horizons	Morphotypes		Totals
	fimbriatus, etc.	*triangulatus*	
4	40	12	52
2d	65	18	83
Totals	105	30	135

TABLE 9.—MORPHOTYPES OF *Monograptus triangulatus;* TYPOLOGICAL CONTINGENCY TABLE FOR THE UPPER THREE HORIZONS, ABSTRACTED FROM TABLE 7

Horizons	Morphotypes		Totals
	fimbriatus, etc.	*triangulatus*	
4+2d	105	30	135
2c	32	7	39
Totals	137	37	174

two beds. The expected frequency for the morphotype *fimbriatus* in Bed 4 is given by

$$E=\frac{105\times52}{135}=40.4.$$

$$\chi^2=\frac{135(40\times18-12\times65)^2}{105\times30\times52\times83}=0.036.$$

With one degree of freedom this gives a P of between 0.8 and 0.9, and the data are not significant.

In considering the next couple, it is permissible to group together the specimens from horizons 4 and 2d, as in Table 9. In this case

$$\chi^2=\frac{174(105\times7-30\times32)^2}{137\times37\times135\times39}=0.330$$

and P falls between 0.5 and 0.7, and the results are once again not significant.

Considering Table 7 in order to choose a third couple for testing, it will be clear that the evidence is inadequate to enable us to apply the χ^2 test to the comparison of horizons 2a and 2b, as the expected frequencies in both the cells of the morphotype *triangulatus* would be below 5. Nor is it possible, for the same reason, to compare these two horizons together with the collection from Bed 2c. It remains possible, however, to halve the table, and either compare the collections from Beds 4, 2d, and 2c with those from Beds 2a and 2b; or from Beds 4 and 2d with those from 2a, 2b and 2c. Table 10 considers this latter alternative, in which

$$\chi^2=\frac{235(105\times9-91\times30)^2}{196\times39\times135\times100}=7.26$$

and P lies between 0.001 and 0.01. In this case we therefore have a significant result.

TABLE 10.—MORPHOTYPES OF *Monograptus triangulatus;* TYPOLOGICAL CONTINGENCY TABLE FOR THE UPPER TWO HORIZONS AND LOWER THREE HORIZONS, ABSTRACTED FROM TABLE 7

Horizons	Morphotypes		Totals
	fimbriatus, etc.	*triangulatus*	
4+2d	105	30	135
2a+2b+2c	91	9	100
Totals	196	39	235

Summarizing this investigation of Challinor's data, we can say that, although a cursory examination of the percentage distribution of the morphotypes suggests a gradual increase of the morphotype *triangulatus* as we move from Bed 2a up the sequence, yet the observations are not conclusive on this score, and only prove that the proportion of *triangulatus* in the lower three beds is less than that in the upper two. To obtain proof that the postulated change was continuous, and to enable one to recognize with certainty with which horizon one was dealing, it would be necessary either to collect more material, or to subject the collections to a finer analysis, and discriminate between the morphotypes *fimbriatus* and *raitzhainiensis*, which Challinor lumped together.

CONFIDENCE LIMITS

When the time comes to draw up the description of a species or subspecies that has been analyzed typologically, it is convenient to do so with reference to the proportions of morphotypes present. Considering the data presented for *Zaphrentites delanouei* (Table 1), it would clearly be possible to specify that the characteristics of the subspecies occurring in the Lower Limestone Group are signified by the fact that out of 679 individuals collected, 5 were of the morphotype *delanouei*, 22 of *parallela*, 474 of *constricta*, and 178 of *disjuncta*. It would not, however, be correct to say that the population consisted of 0.7% *delanouei*, 3.3% *parallela*, 69.8% *constricta*, and 26.2% *disjuncta;* those are the proportions found in the collected sample, not those which actually occur in the population in nature.

Nevertheless, they represent the best estimate we have of the proportions of the population; but just how good is that estimate? Subsequent collections from the same horizons are likely to be characterized by somewhat similar proportions; but just how similar? These questions can be precisely answered by the calculation of the confidence limits. It is first necessary to calculate the standard error of the proportions observed. To do this simultaneously for all four morphotypes is a rather complicated process, and it is more satisfactory to divide the sample into two blocks, in this case 69.8% *constricta* and 30.1% "the rest." We then have to deal with a straightforward case of the binomial distribution, and a sufficiently close approximation to the standard error (s) of the proportion in question (p) in a sample of size N is given by:

$$s=\sqrt{\frac{p(1-p)}{N}}.$$

In this particular case we can calculate the standard error of the proportion of the morphotype *constricta* as being:

$$s=\sqrt{\frac{0.698\times0.301}{679}}=0.0176.$$

The confidence limits of an observed proportion (p) with a standard error (s) are given (to approximately the 95% level of significance) by

$$p\pm2s.$$

If the exact level of significance needs to be calculated (unlikely to be necessary in the field now under discussion) it can always be calculated by consulting tables showing the limits of expectation in binomial distributions (e.g., Fisher & Yates, 1948, p. 48).

In the example now under consideration we have an observed proportion of 0.698, and a standard error of 0.0176. We can therefore say that the proportion of *constricta* in the actual population will probably lie between $0.698\pm2\times0.0176$ (i.e., 66.3% and 73.3%), and will almost certainly lie between $0.698\pm3\times0.0176$ (i.e., 64.5% and 75.1%). The standard error of the proportion of *disjuncta* can also be calculated in the same way.

$$s=\sqrt{\frac{0.262\times0.738}{679}}=0.0169.$$

The standard errors of the rarer morphotypes taken separately seldom give useful results—a sample being characterized more by its main constituents than by its rare varieties, whose proportions vary much according to chance. They may, however, be grouped together, when

$$s=\sqrt{\frac{0.96\times0.04}{679}}=0.0075.$$

The results can be tabulated as in Table 11.

TAXONOMIC DISCRIMINATION

Degree of overlap.—The degree of morphological difference necessary to warrant the distinction of a population as a subspecies is a matter of arbitrary and personal decision. Neontologists commonly adopt some form of the "75% rule" (in which two populations are considered to be subspecifically distinct if more than 75% of one differs from the other; see Mayr, Linsley, & Usinger, 1953, p. 143–144). This "rule" has been applied in most cases, however, to overlap in a single diagnostic character. It is not, therefore, applicable without modification to overlap considered from the point of view of

TABLE 11.—MORPHOTYPES OF *Zaphrentites delanouei*; DERIVATION OF CONFIDENCE LIMITS OF PROPORTIONS IN THE LOWER LIMESTONE GROUP

Morphotypes	Observed numbers	Observed proportions	Standard error	Confidence limits (approx. 95%)
delanouei	5	0.007	0.0075	2.5– 5.5%
parallela	22	0.033	0.0176	66.3–73.3%
constricta	474	0.698	0.0169	23.8–29.6%
disjuncta	178	0.262		
Totals	679	1.000		

morphotypic analysis. The same principles, however, can be applied, and can be demonstrated by reference to Table 12, which shows varying proportions of two morphotypes in seven populations. For paleontological purposes, the following arbitrary scale seems suitable: *if 25% or more of the morphotypes in one population are different from at least 95% of those in another, the two populations may well warrant separation as subspecies.* Thus in Table 12 three subspecies are present, *P*, *Q*, and *R*. But populations 1 and 2 would not be considered worthy of separation as subspecies; nor would populations 3, 4, and 5, or 6 and 7.

The same principle could be applied to specific discrimination thus: *if in two populations no morphotypes are developed in common, they warrant consideration as separate species.* In Table 12, populations 1 and 7 would warrant consideration as separate species, but the association of the transitional populations 2 and 6 would suggest that they were closely related, and circumstances might give reasons for treating them as only subspecifically distinct.

A more complicated case is represented in Table 13, when varying proportions of three morphotypes in three populations are considered. In this case, population 1 would be considered subspecifically distinct from population 2. Population 3 would be considered intermediate between the two other subspecies, and worthy of separation from both as a subspecies on its own account. All three populations would be referred to the same species.

These principles can now be applied to the actual cases under consideration. Table 14 sets out the confidence limits of the proportions of the four morphotypes of *Zaphrentites delanouei* from the four horizons recognized by Carruthers. It will be seen that the population from the Cementstone Group differs subspecifically from that in the Lower Limestone Group, and not quite specifically from that in the Millstone Grit. The distinction between the Lower Limestone Group population and that from the Upper Limestone Group, though statistically significant, would not, according to the arbitrary limits suggested above, warrant discrimination at the subspecific level.

It is instructive to apply similar methods to the taxonomic evaluation of *Monograptus triangulatus* as studied by Challinor. First, it is evident from Challinor's paper that intergradation is extensive between the three morphotypes; we can be sure we are dealing with single chronodemes* at each horizon. Confidence limits are set out in Table 15. Overlap from horizon to horizon is extensive. It is clear that, according to the suggested scale, there is insufficient difference between the populations to warrant the recognition of more than one subspecies.

Such rule-of-thumb methods are of course entirely arbitrary, and it should be emphasized that stratigraphical considerations may require that an important horizon marker should receive greater taxonomic

TABLE 12.—THEORETICAL DISCRIMINATION OF SUBSPECIES ACCORDING TO VARYING PROPORTIONS OF TWO MORPHOTYPES

Populations	Morphotypes		Subspecies
	A	B	
1	0%	100%	P
2	5%	95%	
3	25%	75%	Q
4	50%	50%	
5	75%	25%	
6	95%	5%	R
7	100%	0%	

TABLE 13.—THEORETICAL DISCRIMINATION OF SUBSPECIES ACCORDING TO VARYING PROPORTIONS OF THREE MORPHOTYPES. EACH POPULATION JUST QUALIFIES FOR RECOGNITION AS A SEPARATE SUBSPECIES.

Populations	Morphotypes		
	A	B	C
1	25%	70%	5%
2	5%	70%	25%
3	25%	50%	25%

* A *gamodeme* is an intrabreeding population. As such it is a population of contemporaries. A fossil biocoenose (e.g., a fossil oyster-bed) represents a series of fossil gamodemes in ancestor-descendant relationship to each other. The term *chronodeme* was introduced for such an assemblage of fossils (Sylvester-Bradley, 1951, p. 89), and represents therefore, a gamodeme multiplied by the dimension of time.

TABLE 14.—APPROXIMATE 95% CONFIDENCE LIMITS OF PROPORTIONS OF MORPHOTYPES OF *Zaphrentites delanouei* DERIVED FROM TABLE 1

Horizons	Morphotypes*			
	delanouei	*parallela*	*constricta*	*disjuncta*
Millstone Grit	—	—	[5.0%]	85.3–100%
Upper Lstn. Gp.	—	—[0.3%]	12.0–20.4%	79.2– 87.8%
Lower Lstn. Gp.	2.5–5.5%		66.3–73.3%	23.8– 29.6%
Cementstn. Gp.	64.7–73.5%	21.2–38.8%	[0.9%]	—

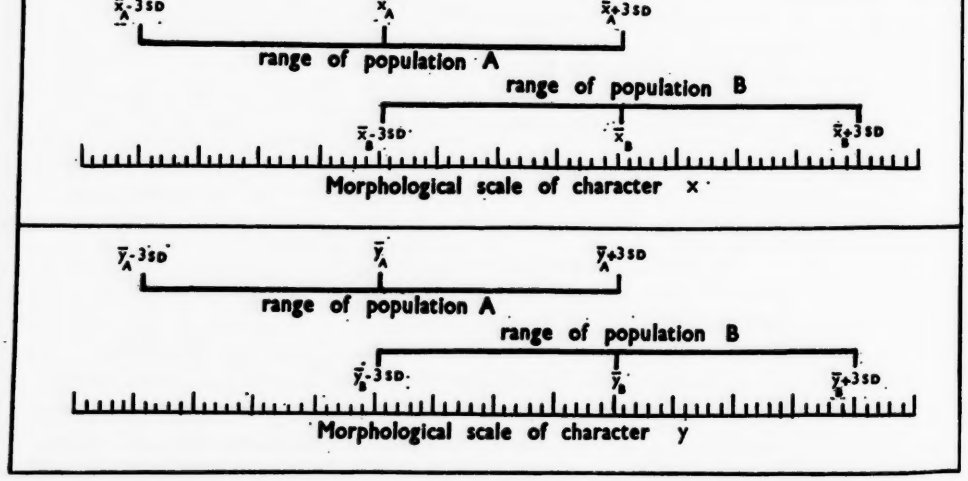
* Confidence limits have not been calculated for the values in brackets.

TABLE 15.—CONFIDENCE LIMITS OF PROPORTIONS OF MORPHOTYPES *fimbriatus*+*railshainiensis* IN FIVE POPULATIONS OF *Monograptus triangulatus*, DERIVED FROM TABLE 7

Horizons	Approx. 95% Confidence Limits
4	65.4–88.6%
2d	68.8–87.2%
2c	69.8–94.4%
2b	86.0–100%
2a	[100%]

discrimination than its morphological analysis would demand.

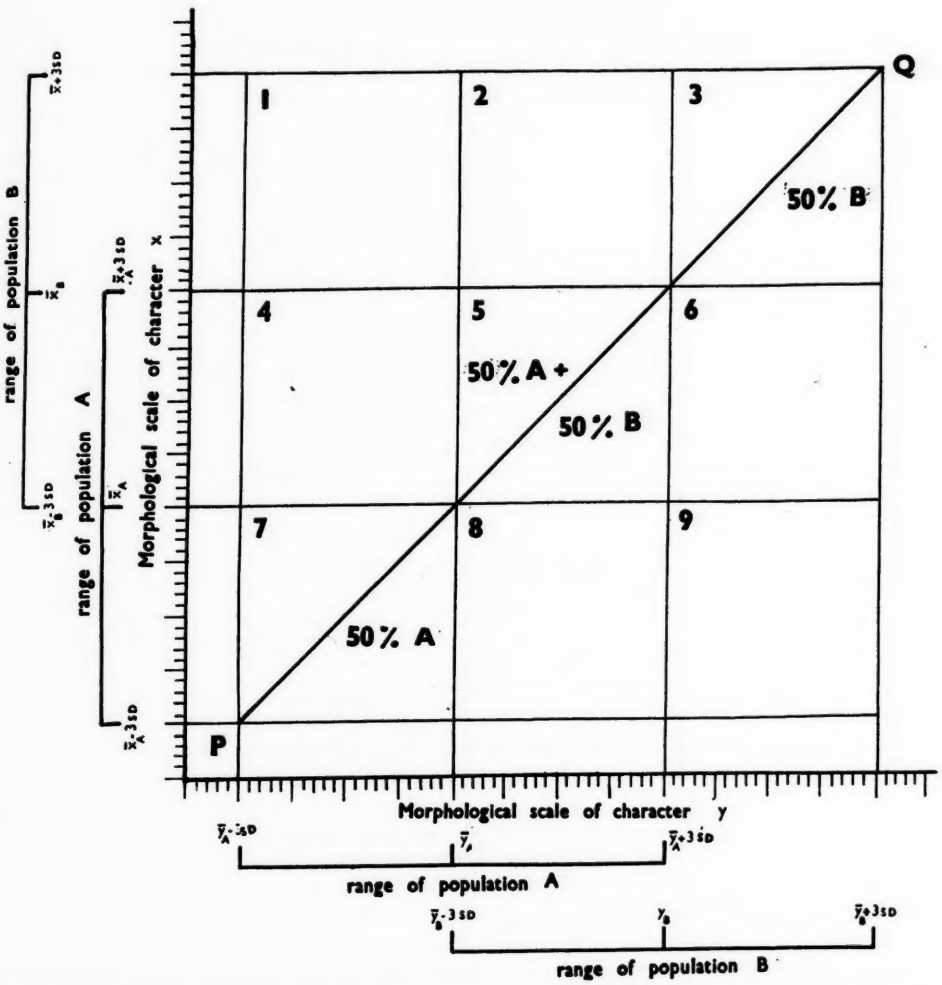
It must also be remembered that a statistically significant difference between two samples, although reflecting a real difference between the *statistical* populations from which they were drawn, may yet not apply to the *biological* populations being studied. Differences may be due to phenotypic modification, to size or shape sorting after death, or to other causes. It is instructive to remember the case of current-sorting on beaches in Trinidad (Martin-Kaye, 1951), in which it was shown that there were significant differences in the proportions of left to right valves in collections of certain lamellibranchs made from different beaches. Size differences between populations are particularly suspect, for they may



TEXT-FIG. *1*—Discrimination between populations. Diagram to illustrate simple case of "50% overlap" in two morphological characters, x and y, of two populations, A and B, when characters are considered separately (univariate analysis). $\bar{x}_A$, $\bar{x}_B$, $\bar{y}_A$, $\bar{y}_B$ signify arithmetic means of populations A and B respectively. The "total range," for the purposes of calculating the overlap, is taken to be six standard deviations. For the sake of simplicity, the standard deviation of each population in each character is considered to be the same. Figs. 2 and 3 illustrate different aspects of the same data when the characters are considered together (bivariate analysis).

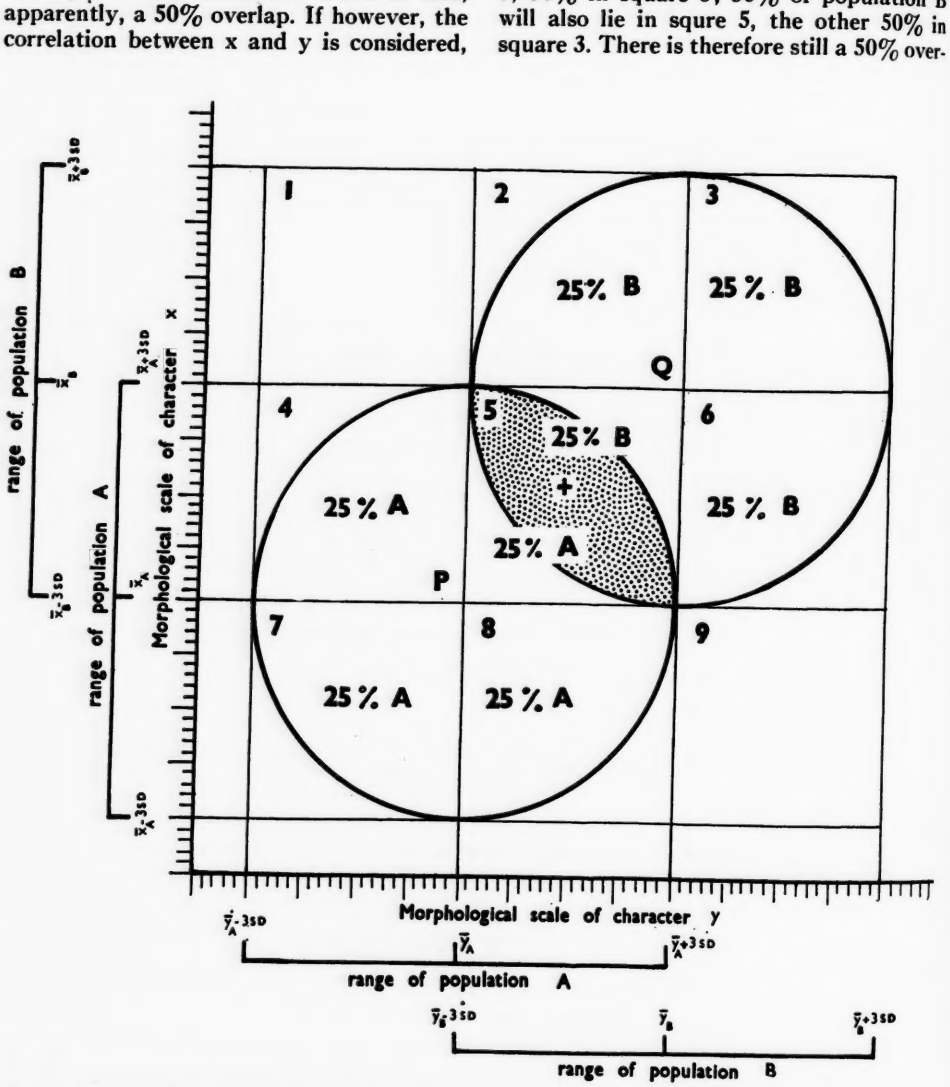
may often be due to sorting, and, if growth is allometric, will be correlated with differences in shape. On the other hand, size is also often an important evolutionary trend. Stratigraphical evidence will usually show whether size differences are paleontologically significant or not.

Multiple characters.—It is necessary to compare methods of taxonomic discrimination as effected by (1) standard quantitative methods, and (2) typological analysis as proposed in this paper. The difficulty of evaluating quantitative differences morphologically is connected with the difficulty of dealing with more than two characters at a time, as has already been discussed above. Any quantitative method of taxonomic discrimination depends on evaluating the degree of overlap there may be between populations. Text-fig. 1 shows how two populations, A and B, have a 50% overlap in both characters x and y, i.e. 50% of population A have the same numerical range in character x as do 50% of population B; the other 50% of A has a range that lies outside the range of population B. The definition of



TEXT-FIG. 2—Bivariate analysis of 50% overlap in two characters with perfect correlation. If the two characters x and y of Fig. 1 have perfect correlation, they will be distributed entirely along the diagonal line PQ. The discrimination between populations will be no finer than when the characters are considered separately.

what is meant by "range" may give diverse interpretations to the expression "50% overlap." For the sake of the present argument the range of each species shown in text-figs. 1–3 can be taken as six standard deviations. Compare Mayr, Linsley, & Usinger, 1953, p. 144. If characters x and y are considered separately, no additional information about overlap is made available—there is still, apparently, a 50% overlap. If however, the correlation between x and y is considered, as in text-figs. 2 and 3, new information about the overlap immediately becomes apparent. In text-fig. 2 the characters x and y are supposed to have a correlation coefficient of 1—i.e., x is always directly proportional to y. The distribution of A and B will then lie on the straight diagonal line PQ. In this case 50% of population A will lie in square 7, 50% in square 5; 50% of population B will also lie in squre 5, the other 50% in square 3. There is therefore still a 50% over-



TEXT-FIG. 3—Bivariate analysis of 50% overlap in two characters with no correlation. If the two characters x and y of Fig. 1 have no correlation, their distribution will lie within two circles with centres P and Q, each with a radius of three standard deviations. Overlap will be restricted to the stippled part of square 5, and will be well below the 25% level.

lap. If, however, x and y are quite uncorrelated (the correlation coefficient is 0), as in text-fig. 3, then the distribution will be different, and show as two clusters of circular extent. 25% of A will lie in each of the squares 4, 5, 7, and 8, and 25% of B in 2, 3, 5, and 6. Only in the stippled part of square 5 will there be overlap, which is therefore reduced to well under 25%.

Two uncorrelated characters taken together therefore afford a much more rigorous discrimination than they do considered apart. Clearly every additional character considered in relation to the others improves the chance of discrimination, hence the value of discriminant functions in multivariate analysis.

Discrimination that makes use of typological analysis in conjunction with contingency tables, however, possesses many of the advantages of such discriminant functions without any of the disadvantages, for all characters may be considered, qualitative as well as quantitative, and the variation displayed by the population can be illustrated with pictures of each morphotype, its relative abundance being indicated by the percentage analysis, with confidence limits established, and the significance of the data calculated by the χ^2 test. An experiment in such an analysis of some Bathonian oysters is presented below.

TYPOLOGICAL ANALYSIS OF SOME BATHONIAN OYSTERS

Introduction

This section illustrates the technique of typological analysis carried out in the study of some of the small ribbed oysters (subgenus *Catinula*) of the Middle Jurassic of Europe. A full description of the investigation will be published elsewhere.

The oysters have been considered to form a single superspecies, divided into three species and a number of chronological and geographical subspecies (Sylvester-Bradley, 1954). For the present purposes it will be sufficient to illustrate how the method has been applied to the study of two collections, representing two chronological subspecies, *Ostrea knorri knorri* and *Ostrea knorri lotharingica*. The former subspecies occurs at a higher horizon and is more restricted in geographical extent than the latter. Where they occur, they are very abundant, and may be collected in handfulls from ploughed fields or vineyards over the outcrop of the beds. They are, in fact, not just water-transported shell-banks, but fossil oyster beds, and as such are biocoenoses (the type example of a biocoenose being an oyster bed). The two collections are, respectively, (1) from the "Knorrithone" (Lower Bathonian) of the hill known as Wartenburg, near Geisingen, in the Schwabian Jura (which is the type locality of *O. knorri lotharingica*); and (2) from the "Varians-Schichten" (Upper Bathonian) of Schönmatt, near Basle, in the Tafel Jura (which is the same horizon as that of the type locality of *O. knorri knorri*, but three kilometers south of it). As in all collections of oysters, there is great variation, and it is first necessary to note how the collections from the two horizons differ from each other. *O. knorri* is then seen to include larger specimens than *O. lotharingica*, the area of attachment typically much larger, and the ribbing slightly coarser (fewer ribs to the millimeter) and slightly greater in amplitude. These, then, must be the characters which are weighted in drawing up arbitrary limits to the morphotypes selected. In order to attain as great a degree of objectivity as possible in the discrimination of morphotypes, it is convenient to construct an analytical key.

Analytical key to morphotypes of two subspecies of Ostrea knorri *(based on left valves)*

1. Greatest dimension of area 5 mm. or more . . 2
   Greatest dimension of area less than 5 mm. . 6
2. Ribbed flank of valve almost straight, inclined at more than 45° to commissure throughout . . . . . morph. A
   Ribbed flank of valve convex, less than 45° to commissure in at least part 3
3. Ribbed flank of valve in part parallel or divergent to commissure 4
   Ribbed flank convergent to commissure throughout . . . . . morph. B
4. Area inclined at 70° or more to commissure . 5
   Area inclined at less than 70° to commissure 7
5. 14 or more ribs to 5 mm. . . . . morph. C
   Fewer than 14 ribs to 5 mm. . . . . morph. D
   No ribs . . . . . morph. E
6. Height 12 mm. or more 8
   Height less than 12 mm. 10
7. 9 or more ribs to 5 mm. . . . . morph. F
   Fewer than 9 ribs to 5 mm. . . . . morph. G
8. 9 or more ribs to 5 mm. . . . . morph. H

Fewer than 9 ribs to 5 mm.....9
Ribs faint, absent in young.....morph. K_1
9. Width less than 5 mm.....morph. J
Width 6 mm. or more.....morph. K
10. 9 or more ribs to 5 mm.....morph. L
Fewer than 9 ribs to 5 mm.....morph. M

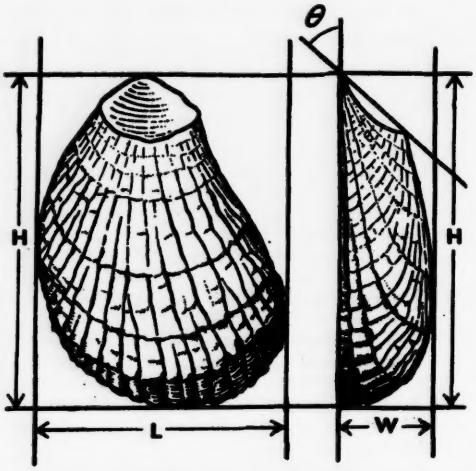
Each morphotype can then be described qualitatively, its quantitative limits defined, and representative specimens (including the holotype) figured.

Systematic descriptions of morphotypes of Ostrea knorri

The diagnosis and description of morphotypes that follows is based only on the two collections now under consideration. In a full investigation it would also be necessary to choose and describe type specimens; this is not now done, as the two collections give an inadequate picture of the total variation displayed by the superspecies, and a full analysis must await publication elsewhere. The morphotypes are illustrated in text-figures 5–15.

Morphotype A

Diagnosis.—Attachment area 5 mm. or more in greatest dimension; ribbed flank of left valve almost straight, inclined at more than 45° to commissure throughout.



TEXT-FIG. *4—Ostrea knorri.* Diagrams to show the direction of measurement of length, height, and width. The term "thickness" is reserved for reference to the thickness of the actual shell material. θ is the angle between attachment area and plane of commissure.

Dimensions (see text-fig. 4).—Length (L), 7–14 mm.; height (H), 9–17 mm.; width (W), 3–8 mm.; greatest dimension of attachment area (A), 5–14 mm.; number of ribs to 5 mm. (R), 6–13; and angle of attachment area to commissure (θ, 8°–40°.

Description.—Attachment area large, exceeding in area that of the rest of the valve, inclined at a gentle angle to commissure. Ribbed flank of left valve short and straight, steeply inclined to commissure, forming a "scarp" to the "dip slope" of the attachment area. Ribbing varied, but for the most part rather fine.

Morphotype B

Diagnosis.—Attachment area 5 mm. or more in greatest dimension; ribbed flank of left valve convex, convergent to commissure throughout.

Dimensions.—L, 9–15 mm.; H, 9–19 mm.; W, 5–12 mm.; A, 6–17 mm.; R, 5–10; and θ, 20°–75°.

Description.—Slightly convex; proportionally wide, with a large attachment area, widest along line joining attachment area and flank. Rather coarse ribs of varying intensity.

Morphotype C

Diagnosis.—Attachment area 5 mm. or more in greatest dimension, inclined at 70° or more to commissure; ribbed flank of left valve convex, in part parallel or divergent to commissure; 14 or more ribs to 5 mm.

Dimensions.—L, 8–9 mm.; H, 10 mm.; W, 5–7 mm.; A, 5–6 mm.; R, 14–20; and θ 70°.

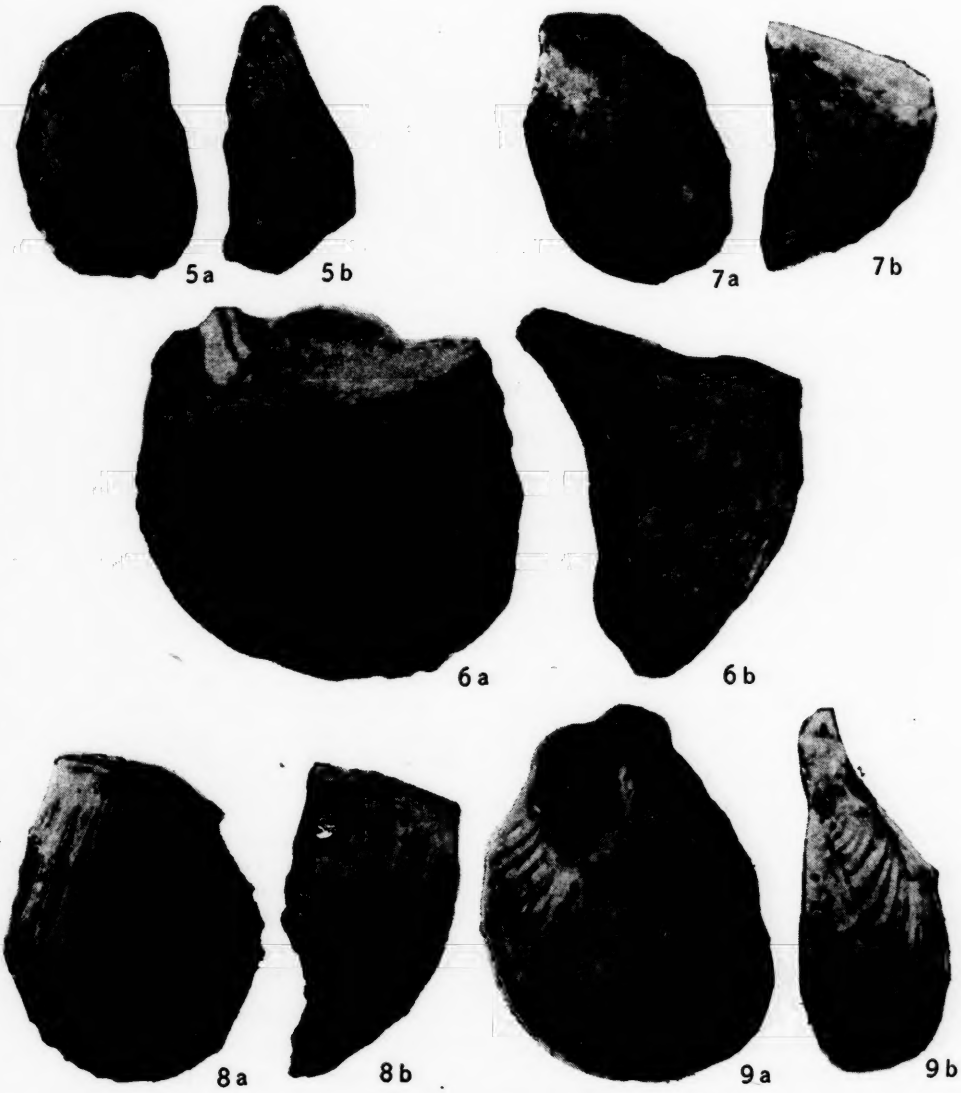
Description.—Small, proportionally wide, markedly convex left valves, with large, steeply inclined attachment area, and finely ribbed flank.

Morphotype D

Diagnosis.—Attachment area 5 mm. or more in greatest dimension, inclined at 70° or more to commissure; ribbed flank of left valve convex, in part parallel or divergent to commissure; fewer than 14 ribs to 5 mm.

Dimensions.—L, 8–12 mm.; H, 8–16 mm.; W, 4–11 mm.; A, 5–11 mm.; R, 6–11; and θ, 70°–100°.

Description.—Strongly convex, with steeply inclined attachment area; propor-



EXPLANATION OF TEXT-FIGS. *5–9**

FIG. *5*—***Ostrea knorri***, morph. A. (spec. no. 3181; Schönmatt); *a*, lateral view; *b*, profile from anterior; ×3.

FIG. *6*—***Ostrea knorri***, morph. B (spec. no. 3086; Schönmatt); *a*, lateral view; *b*, profile from anterior; ×3.

FIG. *7*—***Ostrea knorri***, morph. C (spec. no. 2397; Geisingen); *a*, lateral view; *b*, profile from anterior; ×3.

FIG. *8*—***Ostrea knorri***, morph. D (spec. no. 3152; Schönmatt); *a*, lateral view; *b*, profile from anterior; ×3.

FIG. *9*—***Ostrea knorri***, morph. F (spec. no. 2357; Geisingen); *a*, lateral view; *b*, profile from anterior; ×3.

* Specimen numbers refer to author's collection, which will be presented to the British Museum at a later date. All photographs are by the author.

tionally high, short and wide; strongly and rather coarsely ribbed.

Morphotype E

Remarks.—A morphotype including only one specimen from Geisingen and one from Schönmatt, with same shape as morphotypes C and D, but with no ribs. Possibly examples of another species.

Morphotype F

Diagnosis.—Attachment area 5 mm. or more in greatest dimension, inclined at less than 70° to commissure; ribbed flank of left valve convex, in part parallel or divergent to commissure; 9 ribs or more to 5 mm.

Dimensions.—L, 8–12 mm.; H, 10–15 mm.; W, 3–6 mm.; A, 5–7.5 mm.; R, 9–13; and θ, 30°–60°.

Description.—Proportionally thin, rather large, and, in lateral outline, divergent from umbo (fan-shaped); with large and gently inclined attachment area.

Morphotype G

Diagnosis.—Attachment area 5 mm. or more in greatest dimension, inclined at less than 70° to commissure; ribbed flank of left valve convex, in part parallel or divergent to commissure; fewer than 9 ribs to 5 mm.

Dimensions.—L, 8–14 mm.; H, 12–16 mm.; W, 5–8 mm.; A, 5–12.5 mm.; R, 5–8; θ, 20°–60°.

Description.—Like morphotype F, but proportionally thicker, longer, and more coarsely and more strongly ribbed.

Morphotype H

Diagnosis.—Height over 12 mm.; attachment area less than 5 mm. in greatest diameter; 9 or more ribs to 5 mm.

Dimensions.—L, 9–11 mm.; H, 12–14 mm.; W, 3–5 mm.; A, 1.5–4.5 mm.; R, 9–13; and θ, 60°–80°.

Description.—Like morphotype F, but attachment area smaller and more steeply inclined.

Morphotype J

Diagnosis.—Height 12 mm. or more; width less than 6 mm.; attachment area less than 5 mm. in greatest dimension; fewer than 9 ribs to 5 mm.

Dimensions.—L, 8–12 mm.; H, 12–15 mm.; W, 4–5 mm.; A, 1–3 mm.; R, 4–8; and θ, 40°–80°.

Description.—Like morphotype F, but more coarsely ribbed.

Morphotype K

Diagnosis.—Height 12 mm. or more; width 6 mm. or more; attachment area less than 5 mm. in greatest dimension; fewer than 9 ribs to 5 mm.

Dimensions.—L, 10–11 mm.; H, 13–16 mm.; W, 6–7.5 mm.; A, 3–4.5 mm.; R, 5–7; and θ, 70°–90°.

Description.—Like morphotype J, but wider, not so divergent.

Remarks.—One specimen from Schönmatt (assigned to morphotype "K_1") is like K, but is smooth in the young stage. It becomes faintly ribbed in older stages, the ribbing increasing in strength up to the commissure.

Morphotype L

Diagnosis.—Height less than 12 mm.; attachment area less than 5 mm. in greatest dimension; 9 ribs or more to 5 mm.

Dimensions.—L, 6–10 mm.; H, 8–11 mm.; W, 2–6 mm.; A, 1–4.5 mm.; R, 9–15; and θ, 30°–90°.

Description.—Varied group of small, fine-ribbed forms.

Remarks.—Includes the major part of the collection from Geisingen, distinguished from all that occur at Schönmatt by small size and fine ribbing. Possibly the group may need further subdivision when more extensive collections are analyzed.

Morphotype M

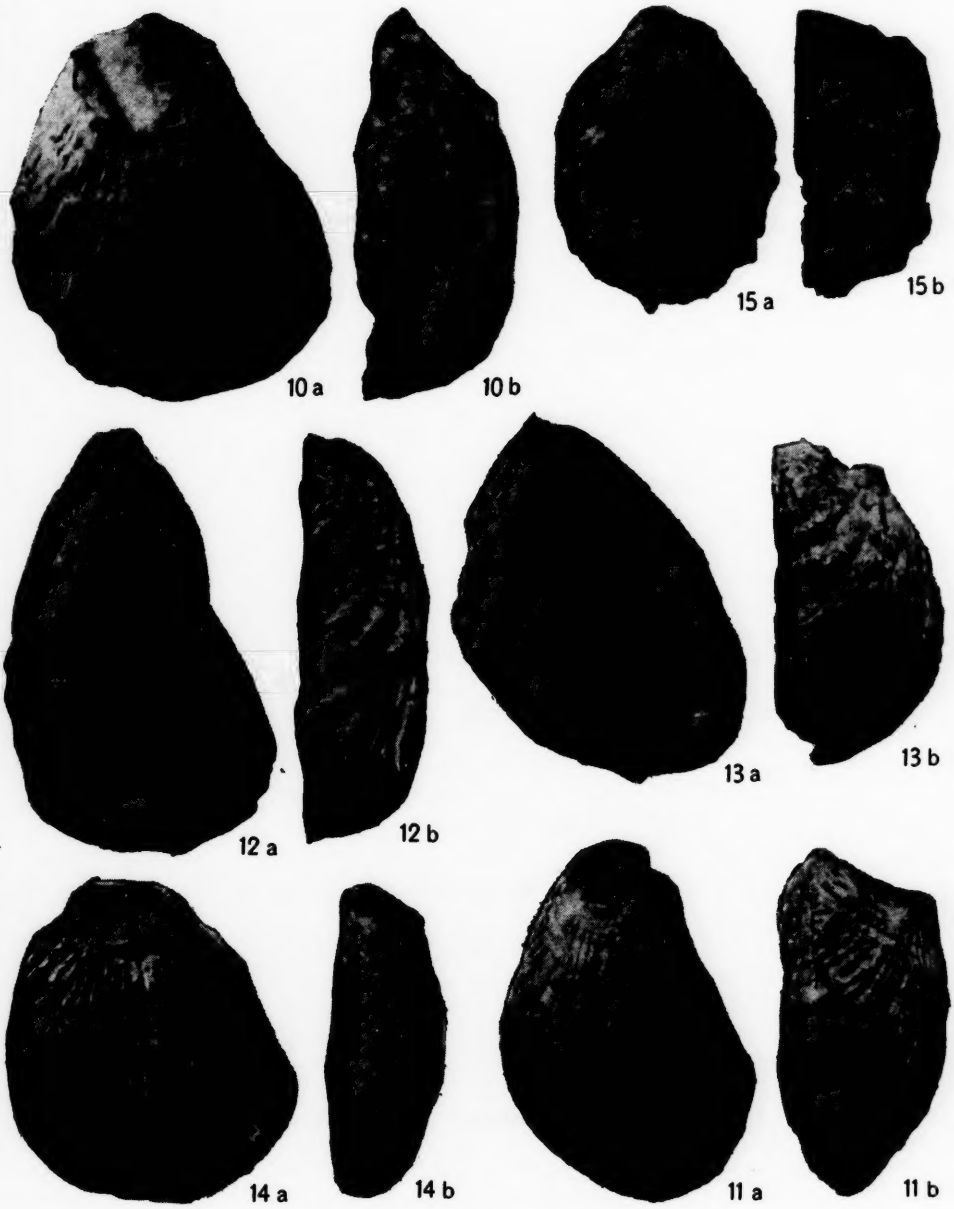
Diagnosis.—Height less than 12 mm.; greatest dimension of attachment area less than 5 mm.; fewer than 9 ribs to 5 mm.

Dimensions.—L, 7–9 mm.; H, 9–11 mm.; W, 5–8 mm.; A, 1.5–5 mm.; R, 6–8; and θ, 60°–100°.

Description.—Small, proportionally high and wide; steeply inclined attachment area; coarse, rather strong ribs.

Discrimination

The description of the species or subspecies can then follow in terms of the proportions of morphotypes present, with confidence limits calculated. Any samples that



EXPLANATION OF TEXT-FIGS. *10–15*

FIG. *10*—*Ostrea knorri*, morph. G (spec. no. 3150; Schönmatt); *a*, lateral view; *b*, profile from anterior; ×3.

FIG. *11*—*Ostrea knorri*, morph. H (spec. no. 2348; Geisingen); *a*, lateral view; *b*, profile from anterior; ×3.

FIG. *12*—*Ostrea knorri*, morph. J (spec. no. 3145; Schönmatt); *a*, lateral view; *b*, profile from anterior; ×3.

FIG. *13*—*Ostrea knorri*, morph. K (spec. no. 3154; Schönmatt); *a*, lateral view; *b*, profile from anterior; ×3.

FIG. *14*—*Ostrea knorri*, morph. L (spec. no. 2347; Geisingen); *a*, lateral view; *b*, profile from anterior; ×3.

FIG. *15*—*Ostrea knorri*, morph. M (spec. no. 3166; Schönmatt); *a*, lateral view; *b*, profile from anterior; ×3.

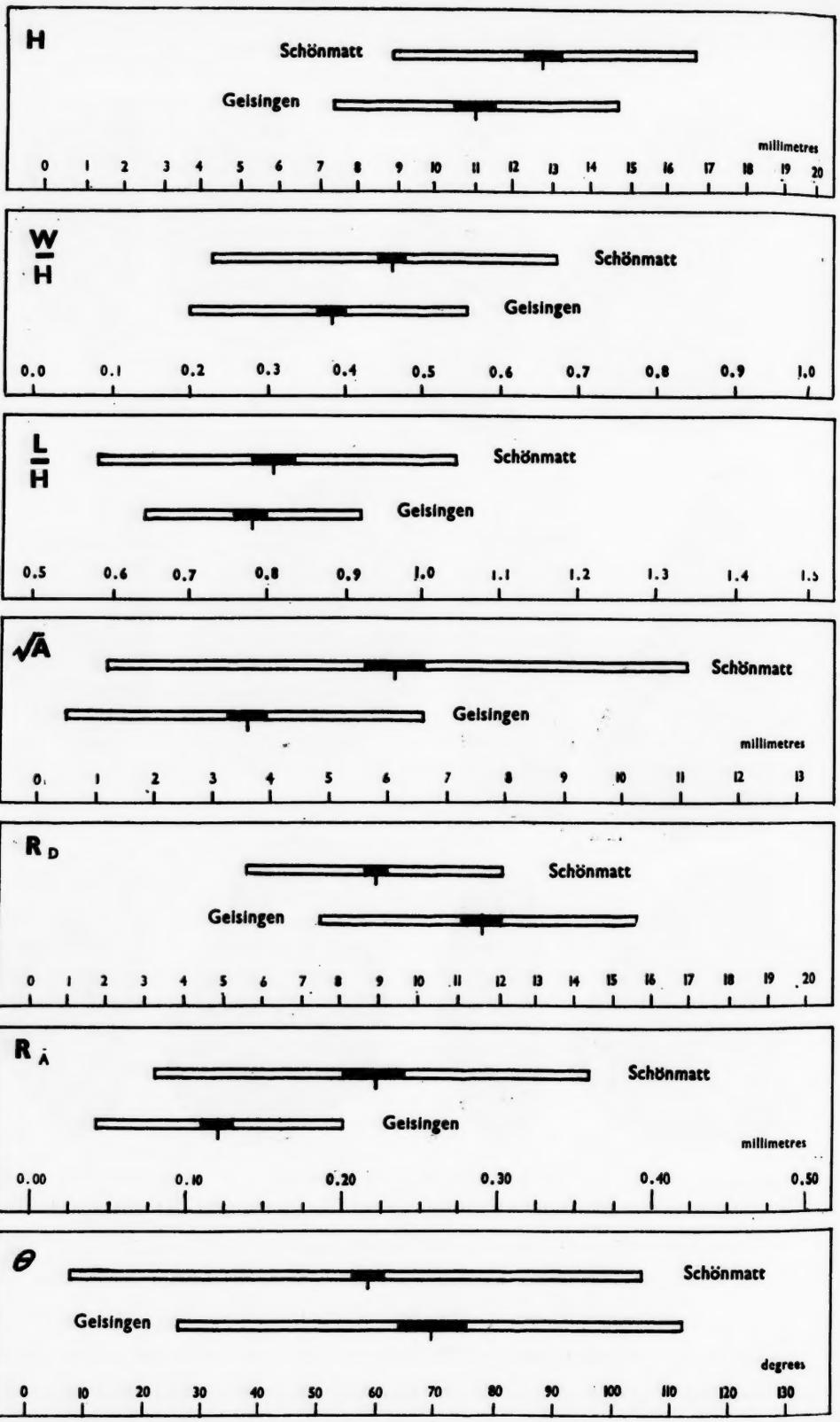

H
Schönmatt
Geisingen
millimetres
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
W/H
Schönmatt
Geisingen
0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
L/H
Schönmatt
Geisingen
0.5 0.6 0.7 0.8 0.9 1.0 1.1 1.2 1.3 1.4 1.5
√Ā
Schönmatt
Geisingen
millimetres
0 1 2 3 4 5 6 7 8 9 10 11 12 13
R D
Schönmatt
Geisingen
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
R Ā
Schönmatt
Geisingen
millimetres
0.00 0.10 0.20 0.30 0.40 0.50
θ
Schönmatt
Geisingen
degrees
0 10 20 30 40 50 60 70 80 90 100 110 120 130

TABLE 16.—TYPOLOGICAL ANALYSIS OF TWO SAMPLES OF *Ostrea knorri* VOLTZ FROM THE BATHONIAN OF SCHÖNMATT (SWITZERLAND) AND GEISINGEN (GERMANY)

Morphotypes	Schönmatt		Geisingen		Totals
D B M	27 14 8	49	0 0 0	0	49
A	20	20	2	2	22
G	21	21	3	3	24
K+K$_1$ J E	5 4 1	10	1 3 1	5	15
F+H	3	3	14	14	17
C L	0 0	0	3 42	45	45
Totals	103	103	69	69	172
χ^2=129.6		Degrees of freedom: 5		P much less than 0.001	

show no significant difference from each other when subjected to the χ^2 test can be grouped together in one subspecies providing other evidence confirms that that is a reasonable postulate. (Two samples may show no significant difference for two reasons—they may be drawn from two populations which are identical, or they may be drawn from two populations which are not identical, but which cannot be told apart because the samples are too small.) In the case under consideration (Table 16), the typological analysis shows such differences that a χ^2 test seems hardly necessary, and cannot fail to produce a highly significant result. It is interesting, however, to compare this result with an analysis by univariate quantitative methods of the same two samples. In Table 17 is an abstract of the statistics of a series of seven characters taken one at a time (univariate analysis). The same data are plotted graphically in text-fig. 16. Although a distinction is apparent between the two samples, they appear to overlap much more strongly than in fact they do—clear evidence that an analysis based on characters taken one or two at a time can be misleading.

Confidence limits

The calculation of confidence limits from the data given of the proportions of morphotypes in the two samples is shown in Table 18. To my mind, this table, taken in conjunction with the figures and descriptions of the morphotypes, gives the reader a more satisfactory paleontological picture of the constitution of these two populations than do the biometrical data expressed in Table 17 and text-fig. 16.

CONCLUSIONS

From considerations discussed in this paper, it is contended that typological analy-

TEXT-FIG. *16*—Graphical presentation of statistics shown in Table 13, showing range of variation exhibited by two collections of *Ostrea knorri* in each of seven characters. Symbols as in Table 17. Lines in full black show range of $M \pm 2\sigma_M$ (i.e., significance of mean). Lines in outline show range of $M \pm 2\sigma$ (i.e., 95% range of variation). These ranges are hypothetical, and only approximate the true values, as in most of the characters studied the variation departs significantly from normal distribution. The discrimination between the two collections is much less satisfactory than that obtained by typological analysis, shown in Table 16.

TABLE 17.—UNIVARIATE ANALYSIS OF SEVEN CHARACTERS OF *Ostrea knorri* AS DEVELOPED IN TWO COLLECTIONS, FROM SCHÖNMATT (SWITZERLAND) AND FROM GEISINGEN (GERMANY)*

		Schönmatt	Geisingen
H	M	12.8	11.0
	$M \pm 2\sigma_M$	12.3 – 13.2	10.5 – 11.5
	$M \pm 2\sigma$	8.8 – 16.7	7.3 – 14.7
W/H	M	0.46	0.38
	$M \pm 2\sigma_M$	0.44– 0.48	0.36– 0.40
	$M \pm 2\sigma$	0.23– 0.67	0.20– 0.56
L/H	M	0.81	0.78
	$M \pm 2\sigma_M$	0.78– 0.84	0.76– 0.80
	$M \pm 2\sigma$	0.58– 1.04	0.64– 0.92
$\sqrt{A}$	M	6.1	3.6
	$M \pm 2\sigma_M$	5.6 – 6.6	3.2 – 3.9
	$M \pm 2\sigma$	1.2 – 11.1	0.5 – 6.6
R_D	M	8.9	11.6
	$M \pm 2\sigma_M$	8.6 – 9.2	11.1 – 12.1
	$M \pm 2\sigma$	5.6 – 12.2	7.5 – 15.7
R_A	M	0.22	0.12
	$M \pm 2\sigma_M$	0.20– 0.24	0.11– 0.13
	$M \pm 2\sigma$	0.08– 0.36	0.04– 0.20
θ	M	56.1	69.4
	$M \pm 2\sigma_M$	51.0 – 61.2	64.2 – 74.6
	$M \pm 2\sigma$	7.1 –105.5	26.4 –112.4

* H is height in millimetres; W/H, ratio of width to height; L/H, ratio of length to height; $\sqrt{A}$, square root of rectangle containing attachment area in millimetres; R_D, rib density in number of ribs per unit length; R_A, rib amplitude in millimetres between crest and trough; θ, angle between attachment area and plane of commissure in degrees. The same data are presented graphically in Fig. 16.

sis, coupled with the specification of named and illustrated morphotypes, accompanied by the calculation of confidence limits, and subjected to tests of significance, affords a more powerful technique for the description of fossil populations than any other current methods of quantitative or qualitative analysis. At the same time the technique is eminently practical, readily comprehensible, and not unnecessarily time-consuming.

Acknowledgments—Dr. G. M. Jowett, Dr. K. A. Joysey, Professor L. R. Moore, and Dr. Dorothy H. Rayner have read the first draft of this paper in typescript. The author is grateful for their criticism, which has been most helpful. It must not be supposed, of course, that they necessarily agree with the methods here proposed. Professor D. H. Valentine offered helpful comments on some of the proposed techniques. Dr. Rayner also prepared the drawings on which text-fig. 4 is based. Dr. Jakob Schweighauser was kind enough to lead the author over the area round Basle in which the specimens from Schönmatt were collected. The University of Sheffield Research Fund made a generous contribution towards the cost of field expenses.

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TABLE 18.—CONFIDENCE LIMITS OF PROPORTIONS OF MORPHOTYPES IN TWO POPULATIONS OF *Ostrea knorri*: *O. k. knorri* AT SCHÖNMATT, AND *O. k. lotharingica* AT GEISINGEN

		Morphotypes					
		D+B+M	A+G	K+J+E	F+H	C+L	Totals
O. knorri knorri	Observed numbers	49	41	10	3	0	103
	Observed proportions (%)	47.6	39.8	9.7	2.9	0	100.0
	Standard error (%)	1.56	1.53		1.00	—	—
	Approx. 95% confidence limits (%)	44.5 to 50.7	36.7 to 42.9		10.6 to 14.6	—	—
O. knorri lotharingica	Observed numbers	0	5	5	14	45	69
	Observed proportions (%)	0	7.2	7.2	20.3	65.3	100.0
	Standard error (%)	—	4.13		4.74	5.73	—
	Approx. 95% confidence limits (%)	—	6.1 to 22.7		10.8 to 29.8	53.8 to 76.8	—

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JOURNAL OF PALEONTOLOGY, V. 32, NO. 1, P. 236–238, 8 TEXT-FIGS., JANUARY 1958

REDESCRIPTION OF *CTENOBOLBINA CLAVIGERA* (JONES) 1891 FROM THE MIDDLE ORDOVICIAN OF OTTAWA, CANADA[1]

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Geological Survey of Canada, Ottawa

ABSTRACT—The beyrichioid ostracod *Ctenobolbina clavigera* (Jones) is redescribed from specimens obtained from the Pamelia beds of the Middle Ordovician Ottawa formation near Ottawa, Canada.

INTRODUCTION

THE beyrichioid ostracod described in this paper is from the Pamelia beds of the Middle Ordovician Ottawa formation. It was originally described as *Beyrichia clavigera* Jones 1891. Study of numerous specimens from strata in the Ottawa Valley indicates the relationship of this species to *Ctenobolbina* Ulrich 1890.

The author is grateful to Dr. A. E. Wilson for bringing the material to his attention, Miss D. Sauriol for preparation of the figure, and the Photographic Section of the Geological Survey of Canada for preparation of the plate.

Specimens have been obtained from black shale beds at three localities in the Ottawa region where they are associated with *Leperditia* cf. *labellosa* (Jones) and *Hallatia?* sp. (Broad Street, Aylmer, Quebec; Buena Vista Road, Rockcliffe, Ontario; and Hogsback on the Rideau River, Ottawa, Ontario), and are reported from one locality in central Ontario at Rush Bay, Wolfe Island, in the St. Lawrence River near Kingston, Ontario.

As described by Jones (1890, 1891) this species was considered to occur in the Chazy group, however, Raymond (1912, p. 353) assigned it to the lower Pamelia formation as follows:

"At the latter locality [Wolfe Island], the limestone holding the *Tetradium* is underlain by a brown and black shale with an abundance of ostracods, among them *Isochilina? clavigera*. This ostracod is abundant in a similar black shale beneath the dark limestone at Ottawa, and it is believed that the shales at the two localities represent the same horizon. If this be so, then the name Pamelia can be adopted for the formation in the Ottawa valley."

As presently known, the species is restricted to lower beds of the Pamelia formation at both localities.

SYSTEMATIC DESCRIPTION

Subfamily SIGMOOPSIINAE? Henningsmoen
Genus CTENOBOLBINA Ulrich
CTENOBOLBINA CLAVIGERA (Jones) 1891

Text-figs. 1–8

Beyrichia sp. Jones 1890, pp. 553–554; *B. clavigera* Jones 1891, p. 65, pl. 11, fig. 7; *B. clavigera clavifracta* Jones 1891, p. 65, pl. 11, fig. 8; *Isochilina? clavigera*, Ulrich and Bassler 1908, p. 281–282, text-fig. 3; *I.? clavigera*, Raymond 1912, p. 353; *I.? clavigera*, Bassler 1915, p. 672; *I. clavigera clavifracta*, Bassler 1915, p. 672; *I.? clavigera*, Bassler and Kellett 1934, p. 338; *I. clavigera clavifracta*, Bassler and Kellett 1934, p. 338.

Carapace subelliptical in lateral view, dorsal and end views unknown. Both valves apparently meeting evenly around the free edge. Greatest height, length, and (probably) width median. Axis from anteromedian to posteroventral parts of carapace. Hingeline straight, slightly more than half as long as greatest length. Anterior and ventral borders evenly rounded; posterior border more narrowly rounded. Posterodorsal border slightly concave, set at an angle of about 140 degrees to the dorsal border.

Each valve with three distinct lobes and a posterior extra lobate area (L4?). L1 broad, reverse-comma-shaped, confluent

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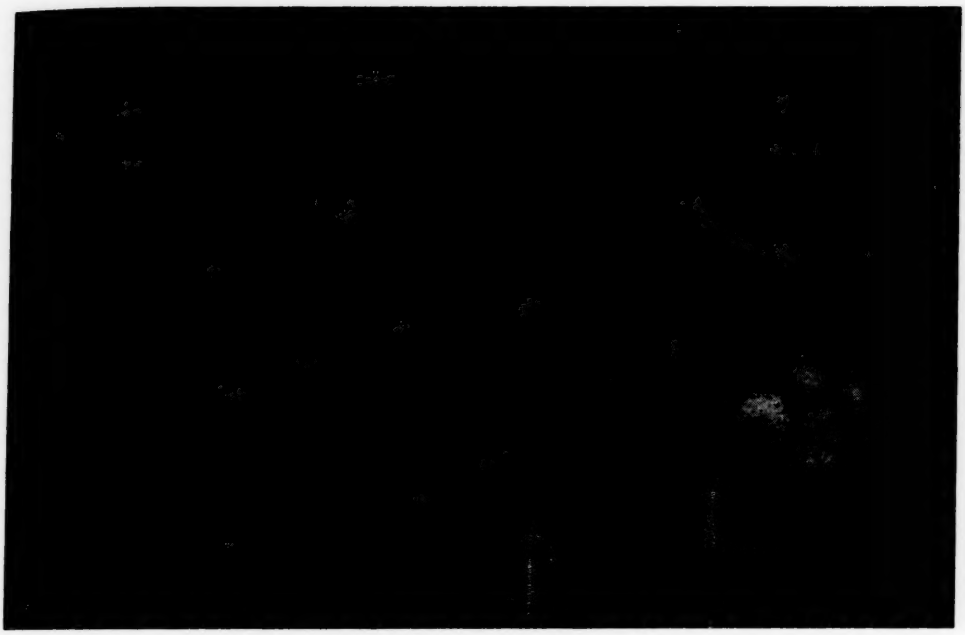


TEXT-FIGS. *1–7*—*Ctenobolbina clavigera* (Jones)
(Magnified about 10 diameters)

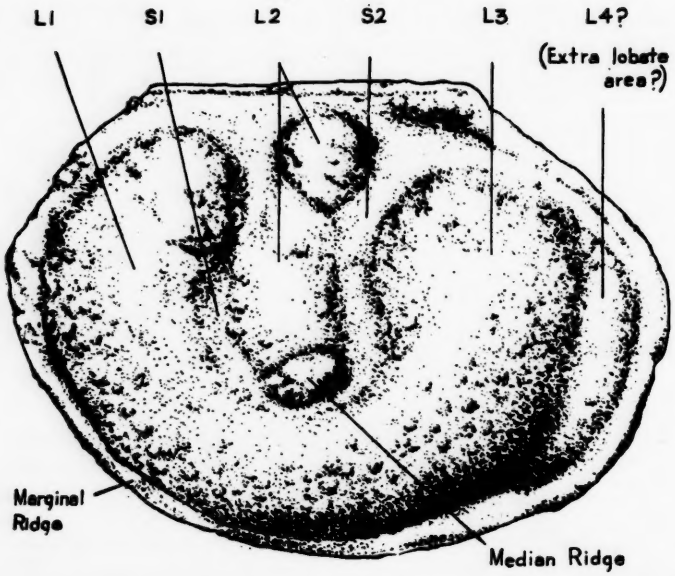
FIG. *1*—Hypotype No. 13604, interior left valve, Buena Vista Road, Rockcliffe, Ontario. *2*, hypotype No. 13605, interior left valve, Hogsback Rapids, Rideau River, near Ottawa, Ontario. *3*, hypotype No. 13606, interior right valve, Broad Street, Aylmer, Quebec. *4*, hypotype No. 13607, exterior right valve, Buena Vista Road, Rockcliffe, Ontario. *5*, hypotype No. 13608, exterior right valve, Broad Street, Aylmer, Quebec. *6*, hypotype No. 13609, exterior right valve, Buena Vista Road, Rockcliffe, Ontario. *7*, hypotype No. 13610, exterior right valve, Broad Street, Aylmer, Quebec.

with broader, comma-shaped L3. L1 with posterodorsal tubercle (eye tubercle of Ulrich and Bassler 1908). L2 divided by a horizontal furrow into two parts. Dorsal part knoblike (text-fig. 6) or partly continuous with ventral part (text-fig. 5). Ventral part curved, almost rectangular, ventrally adjacent to a pronounced median horizontal bar. Median bar as long or longer than width of L2, pointed distally, and separated from the lobate area on all sides by a shallow furrow (text-fig. 3). L3 broad, club-shaped, not extending dorsally as far as L1, joining L1 ventrally of the median bar. Extra lobate area or platform (L4?) crescent shaped, separated from L3 by a furrow parallel with the posterior edge of L3 and extending from the posteroventral margin of the carapace to the posterodorsal marginal ridge. Lobate and extra lobate (?) areas finely granulose or papillose.

Two sulci, convex anteriorly, extending from the smooth dorsal margin to anterior and posterior ends of the median bar, joining the shallow furrow around the median bar.

Marginal ridge broad, complete along free edge and confluent with smooth dorsal area, finely granulose, punctate on inner surface (text-figs. 1,3).

Remarks.—Jones (1891, p. 65) distinguished specimens of *Beyrichia clavigera* from its variety *B. clavigera clavifracta* by the presence in the latter of a small dorsal tubercle on L1 and the division of L2 into two parts. The present writer has seen no specimens lacking a tubercle on L1 nor has a specimen been found without some suggestion of a horizontal furrow dividing L2. It appears likely from Jones' figures (1891, pl. XI, figs. 7,8) that *B. clavigera* was described from steinkerns whereas the figure of *B.*



TEXT-FIG. 8—*Ctenobolbina clavigera* (Jones), Hypotype No. 13624, reconstruction of a complete left valve, about ×45.

clavigera clavifracta represents the external features of the species. The specific description of *C. clavigera* therefore, is broadened to include the original specific and varietal descriptions of Jones.

Types.—Hypotypes Nos. 13604–13610, 13624, Geological Survey of Canada, Ottawa.

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JOURNAL OF PALEONTOLOGY, V. 32, NO. 1, P. 239–241, JANUARY 1958

NEW RECORDS OF PALEOZOIC DIPLOPOD MYRIAPODA

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ABSTRACT—Millipedes with longitudinally grooved tergites of the *Xylobius* type have been found in the early Permian (Arroyo formation) of Texas, and in late Westphalian beds of the Pennsylvanian in Ohio (Upper Freeport coal) and Cape Breton Island, Nova Scotia (above Lloyd Cove coal). Previous records of *Xylobius* from Illinois, Nova Scotia, England and Bohemia are Westphalian in age.

SEVERAL specimens of fossil millipedes have come to light as a by-product of the continuing search for Paleozoic amphibians and reptiles which the Museum of Comparative Zoology is conducting under the direction of Dr. Alfred S. Romer. Dr. O. W. Tiegs had agreed to describe some of this material, but his recent death has deprived us of this valuable contribution. Under the circumstances it seems worthwhile to record the existence of these specimens for the benefit of future workers. The material is now under the care of Dr. H. B. Whittington in the Museum of Comparative Zoology at Harvard College, Cambridge, Massachusetts. Most of the specimens were collected with the assistance of a grant from the National Science Foundation, whose support is gratefully acknowledged.

Three localities and horizons, two in the mid-Pennsylvanian and one in the early Permian, are represented. These will be discussed in descending stratigraphic order.

Coffee Creek, Texas.—MCZ 5451, from the Arroyo formation of the Clear Fork group, Lower Permian (Leonardian). Collected in 1952 by A. S. Romer and party on Coffee Creek, Baylor County, Texas, on the Houston & Texas Central Railroad Survey, Block 2, Section 79. A partial specimen of about 30 segments, 32 mm. long and 27 mm. in circumference, preserved in the round in a concretionary matrix of calcareous reddish silt. Where the surface is exposed the segments are seen to be associated in pairs between which dislocations tend to occur. Superficial, longitudinal (antero-posterior) grooves divide the surface of each tergite into rectangles—the "*frustra*" (read *frusta?*) of Scudder—which are about twice as long as high in the region midway between ends of the specimen. Toward the ends, however, these rectangles appear three to four times as long as high. The upper edge of each rectangle is slightly thicker than the base of the one above it, giving the appearance of inverted shingles. As Fritsch (1899) has pointed out, Scudder was mistaken in assuming the "*frustra*" to be separate little plates. Legs are present in the specimen but are largely obscured by matrix. For a discussion of the ecology of the Arroyo deposits see Olson, 1952.

Linton, Ohio.—Three specimens from a canneloid shale underlying the Upper Freeport coal, Allegheny series (Westphalian D), Pennsylvanian. Collected by D. and L. B. Baird in 1954–55 from the dump of the old Diamond Mine on the west bank of Yellow Creek near its confluence with the Ohio River, in Saline Township, Jefferson County, Ohio. This is the classic Linton locality of Newberry and Cope; its position is incorrectly shown on the maps published by Moodie (1916, fig. 4) and Case (1917, fig. 1). The flattened millipedes are preserved as natural molds in a fine-grained matrix and have been reproduced on high-fidelity latex casts by a process described earlier (Baird, 1955).

MCZ 5268 is the curled posterior part of a millipede with a vertical height (as compressed) of 4 mm. The longitudinal grooves are much more closely spaced than in the preceding specimen, more so even than in *Xylobius pštrossi* Fritsch or *X. mazonus* Scudder, and suggest comparison with *X. frustulentus* Scudder (1890) from Mazon Creek, Illinois. Toward the posterior end the ventral surface and legs are clearly shown. In MCZ 5320, the disrupted sections of

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another individual, an isolated segmental ring measures 3 mm. in diameter. MCZ 5321 is a smaller but complete individual of the same species, 2.2 mm. high and about 25 mm. long.

These Linton millipedes lived around a coal-swamp pool inhabited by a diverse fauna of aquatic vertebrates. Westoll (1944) has analyzed the ecology with special reference to the fish, and a revision of the tetrapod fauna is in process. The millipedes are noteworthy for being the first identifiable invertebrates (aside from *Spirorbis*) in this richly fossiliferous deposit; their discovery thus fills one gap in an evidently incomplete ecological record.

Florence, Nova Scotia.—Three specimens from shale filling the hollow of an upright *Sigillaria* tree which was rooted above the Lloyd Cove (Lower Bonar) coal of the Morien group (Westphalian C), Pennsylvanian. Collected in 1956 by Arnold Lewis and party in the Old Sydney Coal Strippings strip mine No. 7, 2 miles north of Florence, Cape Breton County, Nova Scotia.

In MCZ 5448 the alternate segments bear closely-spaced, rounded grooves which give the surface a horizontally corrugated appearance. In MCZ 5449 the grooves on the tergites are for the most part more widely spaced and the intervening areas are essentially flat, as in the Linton specimens. In MCZ 5450 the segments are separated by deep, rounded grooves and the alternate segments (which are marked off in relatively high rectangles) are convex, giving the body wall a vertically corrugated or reeded appearance. Neither head nor legs is visible in these specimens.

Like the classic specimens which Principal Dawson collected a century ago at Joggins, Nova Scotia, these millipedes had evidently burrowed in the silty humus within the stump of a decayed *Sigillaria* tree and were buried there by accumulating sediment. In the same zone occurs a varied fauna of amphibians and reptiles which had been similarly entrapped. As only a small part of the contents of this tree has so far been exposed in the laboratory, additional specimens of myriapods are anticipated.

Discussion.—On the basis of external characters all the specimens cited above may be assigned to the genus *Xylobius* Dawson, 1860, as redefined by Scudder in 1873 and 1878. Whether all the specimens so assigned by various authors are in fact congeneric is doubtful and remains to be decided by someone trained in the taxonomy of myriapods. In this connection it must be noted that the chief diagnostic characters of living diplopods lie in organs which are rarely preserved in fossils. For the present, however, we may conveniently use the name *Xylobius* to denote a group of diplopods in which the tergites are longitudinally grooved.

This group ranges through much of Westphalian time and recurs in the Leonardian of Texas. Dawson's aptly-named type species *Xylobius sigillariae* is the oldest known, dating from early Westphalian B (Joggins formation). Scudder's species from Mazon Creek, Illinois, fall close to the Westphalian C-D boundary and are much the same age as the MCZ specimens from near Florence, Nova Scotia. Fritsch's exquisitely detailed specimens from the Gaskohle of Nýřany, Bohemia, are nearly contemporaneous with the similarly preserved material from Linton, Ohio (Westphalian D). Woodward (1867) has referred some myriapods from the Westphalian of Great Britain to the genus *Xylobius*. These scattered occurrences, to be sure, give us only a glimpse of the actual distribution of the group in space and time. This note is published in the hope of stimulating further investigation of these rare Paleozoic arthropods.

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JOURNAL OF PALEONTOLOGY, V. 32, NO. 1, P. 242–246, 1 TEXT-FIG., JANUARY 1958

PALEONTOLOGICAL NOTES

NOTE ON TWO FORGOTTEN SPECIES OF PALEOZOIC TABULATE CORALS FROM NEW YORK

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In the summer of 1816 two famous naturalists travelled in New York state: Constantine Rafinesque and Charles-Alexandre Lesueur, the latter in company with William Maclure. Both collected Paleozoic fossils and both later described a few of these, including the famous Ordovician gastropod, *Maclurites*, and several rugose corals (*Siphonophrentis gigantea*, *Heliophyllum corniculum*, etc.). They also published descriptions of two tabulate corals which were overlooked and subsequently described as new species by later workers:

1. *Foerstephyllum striatulum* (Rafinesque)

Tubipora striatula Rafinesque 1817 (September). Am. Monthly Mag. & Critical Rev., v. 1, p. 359–360.

Columnaria alveolata Hall 1847 (*non* Goldfuss 1826). Paleontology, N. Y., v. 1, p. 47, pl. 12, figs. 1,1a,1b,1c (figured specimen from Watertown).

Columnaria ? halli Nicholson 1879 . . . Tabulate Corals . . . , p. 200, pl. 10, figs. 3,3a, text-fig. 29 (species based on Hall, 1947).

Foerstephyllum halli Bassler 1950. Geol. Soc. America, Mem. 44, p. 269, pl. 12, figs. 4–7, pl. 19, fig. 7 (Nicholson's specimens as types).

Rafinesque's description is unusually circumstantial compared with most of his work:

> *Tubipora stiatula.* Tubes connivent, fastigiated, compact, thicker above, nearly straight, hexagonal, unequal, minutely striated, outside and inside.
>
> The specimen upon which this species is ascertained, and which is deposited in the Lyceum of Natural History, was found at Glen's falls on the Hudson river [Saratoga County], imbedded in a calcareous sandstone many feet below the surface of the ground, and nearer to the bed of the river . . . . It is nearly cubical, about five inches long, two or three broad, irregular on the sides, truncated at both ends. The tubes are all compactly connected, through the whole length instead of being only connected by transverse diaphragms, as in the majority of other species; these tubes diverge a little from their base, by growing gradually thicker towards the top, where their broadest diameter reaches two lines [ca. 4 mm.] sometimes; they are slightly flexuous and rather unequal in breadth and length, although their majority forms at the top a truncated plane, not quite even, however. The greatest number are hexagonal, with the sides nearly equal, but may have unequal sides, some are pentagonal, and a few heptagonal, either with equal or unequal sides. The little furrows are slightly flexuous and visible inside as well as outside. They are articulated by internal cells, very visible where the inside is broken and not petrified; it is even sometimes visible outside by slight transverse furrows, and lower cells are shorter vertically than horizontally; the upper ones are generally equal in height and diameter, but some of the uppermost are longer than broad.
>
> This production, as well as the other fossil tubipores, are vulgarly known in the United States under the appellation of *petrified Waspnests*, a faint similarity with some nests of wasps being perceived in many . . . .

From the foregoing it is quite clear that Rafinesque's specimen from the Middle Ordovician (Mohawkian) at Glens Falls was the same as the form later erroneously identified by Hall with Goldfuss' *Columnaria* [*Favistella*] *alveolata* and re-named *C.? halli* by Nicholson. Indeed, some of Hall's specimens came from the same locality. The only other form with which this might be identified is *Favistella alveolata* (Goldfuss), also widespread in the Mohawkian, the holotype of which came also from New York, although actually it seems to have been an erratic from Ontario, but whereas *Foerstephyllum* apparently is a tabulate coral lacking well-developed septa, in *Favistella* the septa are distinct. The presence of septa would hardly have been missed by Rafinesque had his specimen possessed them.

2. *Trachypora vermiculosa* (Lesueur)

Milleporites vermiculosa Lesueur 1821. Mus. Histoire Nat. (Paris), Mém., t. 6, p. 293, pl. 17, figs. 20a,b,c (not d).

Madrepora limbata Eaton 1832 (*non* Goldfuss 1829), Geol. Textbook, p. 39, pl. 5, fig. 52.

Trachypora romingeri Ross 1953. Buffalo Soc.

Nat. History, Bull., v. 21, p. 85, pl. 27, figs. 3–7 (with further synonymy).

Lesueur's description of this ramose tabulate coral, common in the Middle Devonian (Hamilton group) of New York, is easily overlooked, for it appears in the latter part of his well-known paper on Recent corals of the West Indies, and lacks a reference to the figures of a worn specimen on plate 17:

> On peut, je crois, ranger parmi les millépores de M. Lamarck une espèce de polypier rameux dont j'ai trouvé one portion sur les bords du lac Erié, avec des térébratules, etc.
>
> Ce polypier est rameux, cylindrique, compact, à surface granuleuse et perforée de nombreuses cellules rondes, sans rayons, sans dentelures ni stries intérieures pressés, et sans ordre à la surface des rameux.
>
> La couleur est noirâtre; la surface est couverte de petites élévations granulaires; les cellules sont assez rapprochées.

The only reference I have found to this species of Lesueur is by Milne-Edwards & Haime (1860, p. 238), who thought it might be a *Heliolites*. Lesueur's specimen undoubtedly came from the famous fossil locality on the shores of Lake Erie in the vicinity of 18-Mile Creek, erroneously indicated as one locality for *Maclurites* in Lesueur's account of that form in 1818:

> . . . In another stratum is found the Alcyonite, Trilobite, a Terebratula with flat valves, a Favosite, etc.; and a large discoidal shell, which more particularly forms the subject of this paper, and which at first sight resembles an Ammonite, or Nautilus; and was noticed as such by Mr. Maclure in his geological observations, p. 27. We [Lesueur & Maclure] first observed an impression of it in the compact limestone [Tichenor limestone member of the upper Hamilton] which forms a portion of the bank of Lake Erie, near Eighteenmile crick, mixed with Caryophilloea [sic], and subsequently at Basin Harbour, on Lake Champlain . . . .

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NEW NAME FOR AN ORDOVICIAN SHALE IN MANITOBA*

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The name Stony Mountain formation as first defined by Dowling (1900, p. 46 F) applied to beds of Richmond age in southern Manitoba comprised two lithically distinct sets of beds: red shales and overlying "thick-bedded limestones." The fauna, almost entirely derived from the shales, was described by Whiteaves and by Ulrich. Okulitch (1943) reviewed the fauna, added to it, and named four units within the formation: (1) Stony Mountain shale member, (2) Penitentiary member, (3) Gunton member and (4) Birse member. Units 2 and 3 correspond to Dowling's limestones, but the dolomites of the Birse member had previously been considered to be Silurian. Re-

* This note is published with the permission of the Deputy Minister Department of Mines and Technical Surveys, Ottawa.

cently Stearn (1956) has shown that the still higher Stonewall "Silurian" dolomites contain Ordovician fossils. Stearn considered the Stonewall formation to be post-Stony Mountain, but others (Ross, 1957, p. 446) have extended the term Stony Mountain to include these beds.

Unnecessary confusion is introduced into discussion of these beds and of their correlants, by the dual use of the term Stony Mountain for the formation and also for the most fossiliferous member within it. The "Stony Mountain fauna," which has become well known and recognized over a large area, is not the fauna of the formation, but only of the lower part of it.

It seems expedient that a distinctive name be proposed for the Stony Mountain shale member of Okulitch, and we suggest that it be called the Gunn member of the Stony Mountain formation. It is thought to be 75 feet thick, but only the upper 15 feet are exposed on the surface. At present it is best seen in a quarry on the grounds of the Stony Mountain penitentiary, and in cuts along adjacent roads. The originally described type section, at the quarry operated by the City of Winnipeg a short distance to the north (known in Dowling's time as the Gunn quarry) is still available, but shows only a vertical face which is more difficult to study. The member and its relationships have been recently described by Baillie (1952), with a good summary of earlier work.

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MANUSCRIPT RECEIVED JUNE 22, 1957

OCCURRENCE OF GLASS SPONGES IN THE DEVONIAN OF WEST VIRGINIA

NOLAN E. RICE
Department of Biology, University of Richmond

In April, 1956, and again in 1957, geology students of the University of Richmond found fossil glass sponges in rocks of the Chemung Formation (Upper Devonian) in West Virginia. Altogether about two dozen specimens were collected, most of them fragments, but several were fairly complete. One of these was deposited in the United States National Museum in Washington. It was identified as *Hyphantaenia chemungensis* Vanuxem by Dr. G. Arthur Cooper, Head Curator of Geology.

The fossil sponges occur in heavy-bedded shaly sandstones which are exposed on the face of a cut on the left side of U. S. Highway 250, a distance of 8.2 miles south of the city limit sign of Elkins, West Virginia. Although the entire exposure was examined carefully, fossils were found only in several adjacent strata. Because of the dipping structure, the fossiliferous strata at one end of the cut are only a few feet above the shoulder of the highway, but at the other end some thirty or forty feet.

Some of the specimens measure up to ten inches in diameter. They are slightly convex (or concave, depending on the view) impressions consisting of a series of as many as fifteen equidistant, concentric, narrow bands crossed by thirty or more radial bands. This species is also found in the "Chemung Formation" in New York State. Excellent illustrations appear in *The Paleozoic Reticulate Sponges, New York State Museum, Memoir 2, 1898.*

An examination of *Volume 15* of the *West*

Virginia Geological Survey Publications (WOODWARD, HERBERT P., *Devonian System of West Virginia, 1943*) reveals the occurence of *Hindia* (*sphaeroidalis*) *inornata* Duncan in the Helderberg Formation and unidentified sponge spicules in the Huntersville Formation, but no record of the presence of *Hyphantaenia chemungensis* is shown in the check-lists of Lower, Middle, and Upper Devonian Faunas. Therefore, it appears quite likely that the present report is the first of the occurrence of this sponge in the Devonian of West Virginia and the third species to be found in that system.

MANUSCRIPT RECEIVED AUGUST 2, 1957

THE TYPE OF *PHLEGETHONTIA LINEARIS* COPE

A NOTICE THAT BOTH PLATE AND COUNTERPLATE ARE PRESERVED IN THE AMERICAN MUSEUM OF NATURAL HISTORY COLLECTIONS

WILLIAM D. TURNBULL
Assistant Curator, Fossil Mammals, Chicago Natural History Museum

While examining the American Museum's Linton, Ohio collection of Pennsylvanian vertebrates in connection with the preparation of a report of a *Phlegethontia* from Illinois, (Turnbull & Turnbull, 1955), it was discovered that the type of *P. linearis* Cope was preserved both as plate and as counterplate though no indication of this fact was found in the literature. Cope first mentioned *P. linearis* in 1871 without illustration or proper description, and again in 1874 with the same deficiency. In 1875 he described the specimen briefly, (p. 367 & pl. 43) and gave an accompanying illustration. From this illustration it is certain that AMNH #6966, (Newberry Coll. #8369G) is indeed the portion that Cope designated as the type, though it apparently had not been given its Newberry number in 1875 when Cope described it. In 1930 Romer, (p. 86) listed AMNH #6886 as the type of *P. linearis* and the American Museum catalogue entries agree with this, and give in addition the old Newberry #8467G. Gregory (1948, p. 657) followed Romer and cited AMNH #6886 as the type, but he also mentioned AMNH #6966 as an additional specimen. Thus it appears that Cope, Romer and Gregory were all unaware that both plate and counterplate existed in the collection.*

The photographs (text-fig. 1) illustrate how these two portions are in reality parts of the same specimen. Note the mirror-image position of the skull and the much coiled vertebral column in both plates. Also, the presence of a tiny paleoniscid fish, (P), and the nearness of fit of the plates adds further support to the argument. These facts combine to leave no trace of doubt that the two "specimens" represent the same individual, preserved in plate and counterplate, and that therefore both are portions of the type.

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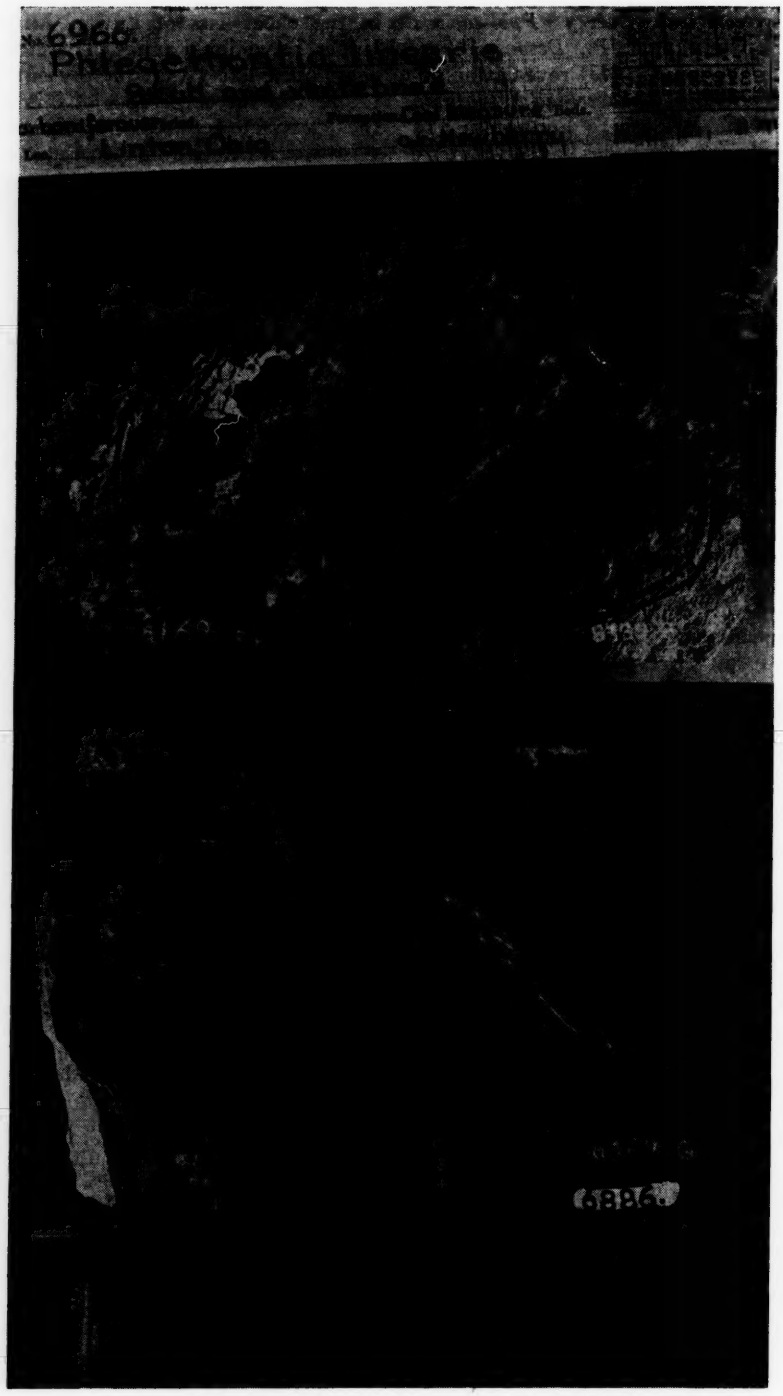
* Mrs. Rachel Nichols of the AMNH staff has now assigned AMNH #6886 to the entire specimen for future use, in keeping with the type designations given by Romer and by Gregory.

(*Text-Fig. 1 on next page*)



TEXT-FIG. *1*—Plate, AMNH #6966, and counterplate, AMNH #6886, of the type of *Phlegethontia linearis* Cope.

JOURNAL OF PALEONTOLOGY, V. 32, NO. 1, P. 247, JANUARY 1958

NOMENCLATURAL NOTES

ASTROCOENIA BARRANQUINIANA, A NEW NAME FOR *ASTROCOENIA MINIMA* VON DER OSTEN

ERIMAR VON DER OSTEN
Ministerio de Minas e Hidrocarburos, Caracas, Venezuela

In a recent paper "A fauna from the Lower Cretaceous Bsrranquin formation of Venezuela," the name *Astrocoenia minima* was proposed for a new coral species.

Dr. J. W. Wells has kindly called my attention to the fact that his name is preoccupied by a Lower Cretaceous French coral. I propose the name *A. barranquiniana* von der Osten, for the Venezuelan species.

TYPE SPECIES FOR THE NEMERTAN WORM GENUS, *LEGNODESMUS*

B. F. HOWELL
Princeton University, Princeton, N. J.

In Palaeontographica, v. 17, 1869, p. 174, pl. 36, figs. 6–8, and pl. 37, figs. 1,2,4, and 5, E. Ehlers proposed and figured a new genus of worms, *Legnodesmus*, but did not name any species, so that the genus has lacked a type species. It is here proposed to name the worm which Ehlers described and figured *Legnodesmus ehlersi*. This species will thus be the genotype of the genus. The holotype is the specimen shown in figure 6 of Ehler's plate 36.

SULCOCEPHALUS WILSON 1948 TO REPLACE *BERKEIA* RESSER, 1937, AND *BURNETIELLA* TO REPLACE *BURNETIA* WALCOTT, 1924

CHRISTINA LOCHMAN
New Mexico Inst. Mining and Technology, Socorro, New Mexico

Burnetia Walcott, 1924 (Smithsonian Misc. Coll., v. 75, no. 2, p. 54) is a junior synonym of *Burnetia* Broom 1923 (Proc. Zool. Soc. London, 1923, p. 661, 671) for a South African Karroo reptile. I propose *Burnetiella* to replace *Burnetia* Walcott 1924, genotype—*Ptychoparia? urania* Walcott, 1890 (Proc. U. S. Nat. Mus., v. 13, p. 274).

In 1937 C. E. Resser proposed the genus *Berkeia* (Smithsonian Misc. Coll. v. 95, no. 22, p. 3) for a Franconian trilobite previously described by Berkey from the Ironton formation at Taylors Falls, Minnesota. Inadvertently, Resser cited the genotype of *Berkeia* as *Agraulos convexus* var. B Berkey, although he and subsequent workers were agreed that the specimens represented by Berkey's var. B did not belong to the species *Agraulos convexus* Whitfield to which Berkey had referred them. Resser in the same publication redescribed the specimens of var. B as *Berkeia typica* Resser. However, Ulrich & Resser (Trans. Wis. Acad. Sci., Arts and Letters, v. 21, p. 94, July 1924) had designated *Arionellus* (*Agraulos*) *convexus* Whitfield, 1878 as the genotype of their genus *Camaraspis*. Consequently, *Berkeia* becomes a junior synonym of *Camaraspis*.

In 1948 J. L. Wilson described the genus *Sulcocephalus*, genotype—*Talbotina candida* Resser, 1942 (Jour. Paleontology, v. 22, p. 31, pl. 8, figs. 1,2). *Sulcocephalus candida* (Resser) and *Berkeia typica* Resser were recognized as congeneric by Lochman (1953) and thus *Sulcocephalus* is the first name available for this generic group.

REFERENCE

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REVIEW

TREATISE ON MARINE ECOLOGY AND PALEOECOLOGY, Volume 2. PALEOECOLOGY, Harry S. Ladd, Editor. Geol. Soc. America, Mem. 67, 1077 p., illus., 1957. $10.00.

Particularly in the youthful stages of any science, a compendium is extremely important and useful. It summarizes the achievements, appraises the methods, and points out the present limitations of knowledge and the unexplored areas. Those in the science are offered a chance to take stock. The onlookers can see what the science is about, what it has done, and what it hopes to do.

The *Paleoecology* volume of the Treatise on Marine Ecology and Paleoecology is such a compendium. It brings together in 24 chapters and an annotated bibliography the contributions of 75 authorities, each writing in his special field. The remarkable continuity from one chapter to the next must be credited to the editorial work of Dr. Ladd. The table of contents and the list of contributors tell a story of careful planning for the volume; unfortunately, they are too long to be included here. Instead, let us look at the three major divisions.

"The Paleontological Record and the Origin of Life" includes the first six chapters. In addition to the introduction, this division discusses the nature of paleontological evidence, the history of development of marine paleoecology, the current ideas on the origin of life, the organic constituents of fossils and their possible uses, and a classification of marine environments. These are indeed stimulating subjects. Every paleontologist must devote serious study to them if our science is to mean more than "bone and stone." As the volume stresses, new approaches are earnestly sought to get the maximum information about the past from the fossils and their occurrence. The assessment of paleoecology fills an urgent need at this time.

"Selected Analyses from the Geologic Record," the second division, includes Chapters 7 through 24, with 589 pages, numerous plates, figures, charts, and maps. Here applied examples of paleoecologic study and technique are given for each geologic period. The division ends with a chapter on *Future of Marine Paleoecology*. Of course, neither all epochs nor all areas of the world can be covered in one book; as one is made aware, not all have been investigated. Each example is a paleoecologic analysis restricted to one formation, one province, one epoch, or one type of environment. In this way, however, the reader learns about not only the particular problem and the author's solution, but also the current criteria and methods and such diverse paleoecologic topics as reefs, dwarfed faunas, environmental control of fauna, and relationships between tectonic movements and faunas.

The volume concludes with an "Annotated Bibliography of Paleoecology," which is actually 53 separate bibliographies arranged by plant, invertebrate, and vertebrate taxa. This organization of reference material seems ideal. Paleontologists are more often concerned with fossils of a particular taxon than with all the fossils of a certain age. In this division, they will readily find references to previous paleoecologic interpretations for the fossils which they are investigating. The bibliography for each taxon is introduced by a discussion of how this group of fossils is presently used for deciphering ancient geography, temperatures, depths of seas, and animal communities. Indirectly, each bibliography presents a history of paleoecologic thought on the taxon. Much remains to be studied. Some of the bibliographies are rather brief.

This publication culminates work started in 1940 by the late Dr. T. Wayland Vaughn. He organized the Subcommittee on the Ecology of Marine Organisms as part of the Committee on Geologic Research, which in 1942 became the Committee on Marine Ecology as Related to Paleontology and is now known as the Committee on Marine Ecology and Paleoecology. As early as 1941 an ecological treatise was planned. The war years curtailed much of the program, and the Committee personnel changed. In 1948 the Committee stabilized at 19 members

and has so remained. In 1951, because of failing eyesight, Dr. Vaughn asked to be dropped from the Committee. He died the following year. It is most fitting that the volume is dedicated to this great paleontologist, who so steadfastly worked toward it.

ROBERT V. KESLING
Museum of Paleontology
University of Michigan

NOTICES

The International Trust for Zoological Nomenclature has pleasure in announcing that arrangements have been made for the immediate publication in book-form of the first instalment of each of the "Official Lists" of valid zoological names and of the corresponding "Official Indexes" of rejected and invalid names, together with the first instalments of the "Official Lists" of works approved as available for zoological nomenclature and of the "Official Index" of rejected and invalid works. The categories of names covered by these "Lists" and "Indexes" range from specific names to ordinal names. The total number of entries contained in the instalments now to be published amounts to about five thousand.

The first of these "Lists," that relating to generic names was established by the Ninth International Congress of Zoology, Monaco, 1913, while the most recent were brought into existence by the Fourteenth Congress at Copenhagen in 1953. The entries made on these "Lists" and "Indexes" have been promulgated from time to time by the International Commission on Zoological Nomenclature in individual "Opinions" and "Directions" but owing to the large number of documents so involved it has become increasingly difficult for specialists to ascertain what names have so far been registered under this system. This difficulty will completely disappear on the publication of the installments now in the press, each of which will be supplied both with a full alphabetical index and also with alphabetical indexes arranged by major groups. The groups so selected will normally be Classes but in the case of large Classes containing well-recognized Orders, those supplementary indexes will be on an ordinal basis.

These "Official Lists" and "Official Indexes" constitute the principal instrument devised to promote stability in zoological nomenclature and will be indispensable to all specialists engaged in taxonomic work in zoology and palaeontology.

All enquiries in regard to the above publications should be addressed to the International Trust for Zoological Nomenclature at its Publications Office (41 Queen's Gate, London S.W.7.).—FRANCIS HEMMING

COPIES OF SYMPOSIUM FOR SALE

DISTRIBUTION OF EVOLUTIONARY EXPLOSIONS IN GEOLOGIC TIME, Jour. Paleontology, v. 26, no. 3, May 1952.

Copies of this Symposium are available in paper covers at a postpaid price of $2.00 each for single copies, or $1.75 each in lots of five or more. Prepaid orders should be addressed to the Secretary, H. B. Whittington, MCZ, Harvard University, Cambridge 38, Mass.

INTERNATIONAL PALEONTOLOGICAL UNION

London Session, July 1958

A meeting of the International Paleontological Union has been scheduled during the forthcoming International Congress of Zoology and the Colloquium on Zoological Nomenclature. It is hoped that paleontologists present at the Congress will thus be able to further international paleontology by strongly presenting their views and by receiving an interim progress report on I.P.U. by the Secretary, J. Roger. Paleontological field trips may possibly be scheduled if sufficient interest is expressed.

It has not been possible to incorporate the London meetings of I.P.U. into the official program of the Congress. Notifica-

tions of the time and place of the meetings will be disseminated during the Colloquium (July 9th–15th) and the Congress (July 16th–23rd). Paleontologists proposing to attend should register now with The Registrar, XVth International Congress of Zoology, c/o British Museum (Natural History), Cromwell Road, London, S.W. 7, and complete the form obtainable from Dr. Harry B. Whittington, Museum of Comparative Zoology, Harvard University, Cambridge, Mass.

SOCIETY RECORDS AND ACTIVITIES

"By special action of the Council on November 3, 1957 article 3, chapter 1, of the by-laws of the Paleontological Society were suspended so that the following could be admitted at once to membership"

ASH, SIDNEY R., 715 Montoya Road NW, Albuquerque, New Mexico: Stuart A. Northrop, Christina Lochman Balk

BLACK, CRAIG CALL, 34 Amity Street, Amherst, Mass.: Albert E. Wood, Donald Baird, Alfred S. Romer

BOLTON, THOMAS ELWOOD, Geological Survey of Canada, Department Mines and Technical Surveys, Ottawa, Canada: G. Winston Sinclair, Murray J. Copeland

BRODKORB, PIERCE, Department of Biology, University of Florida, Gainesville, Fla.: H. K. Brooks, Jackson Lewis

BURCKLE, LLOYD H., 487 N. 3E, Provo, Utah: J. Keith Rigby, Harold J. Bissell

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FUNKHAUSER, JOHN WILLIAM, 4971 E. 26th Street, Tulsa 14, Oklahoma: William R. Evitt, Lewis E. Stover

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KAUFFMAN, ERLE GALEN, Museum of Paleontology, University of Michigan, Ann Arbor, Michigan: Erwin C. Stumm, Robert V. Kesling, G. M. Ehlers

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LUMSDEN, WILLIAM WATT, JR., 10847 Strathmore Drive, Los Angeles 24, California: W. P. Popenoe, Peter D. Rodda

MALIN, EUGENE ROBERT, 210 North 13th Street, Lincoln, Nebraska: Walter Sadlick, John A. Howe, T. M. Stout

MOHAN, KRISHNA, c/o State Museum, University of Nebraska, Lincoln 8, Nebr.: Walter Sadlick, T. M. Stout

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OELRICH, THOMAS MANN, Department of Anatomy, East Medical Building, Univ. of Michigan, Ann Arbor, Mich.: Erwin C. Stumm, Lewis B. Kellum, Claude W. Hibbard

PALMER, ALLISON RALPH, Room 333 U. S. National Museum, Washington 25, D. C.: Robert B. Neuman, Raymond C. Douglass, Ellis L. Yochelson

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ROGERS, KENNETH JOSEPH, Box 211BB, Route 2, Breaux Bridge, La.: Robert V. Kesling, Erwin C. Stumm, G. M. Ehlers

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TAYLOR, DWIGHT WILLARD, 338 U. S. National Museum, Washington 25, D. C.: John B. Reeside, Jr., Claude W. Hibbard, Erwin C. Stumm

TOZER, EDWARD TIMOTHY, Geological Survey of Canada, Department Mines and Tech. Surveys, Ottawa, Canada: G. Winston Sinclair, D. J. McLaren

WEIGEL, ROBERT DAVID, Department of Biology, University of Florida, Gainesville, Fla.: Robert V. Kesling, Claude W. Hibbard, Erwin C. Stumm

WESTERMANN, GERD ERNST GEROLD, 75 East Street, Dundas Ontario, Canada: Bernhard Kummel, H. B. Whittington

NOMINATIONS FOR OFFICERS IN THE PALEONTOLOGICAL SOCIETY FOR 1958–1959

In accordance with the provisions of Chapter III, Section 2 of the By-Laws, the Council of the Paleontological Society announces the following nominations for the offices in the Society for 1958–59:

For President: FRANK M. SWARTZ, University Park, Pennsylvania

For Vice-President: WILLIAM R. EVITT, Tulsa, Oklahoma

For Secretary: HARRY B. WHITTINGTON, Cambridge, Massachusetts

For Treasurer: CLAUDE C. ALBRITTON, JR., Dallas, Texas

For Editor: ERWIN C. STUMM, Ann Arbor, Michigan

In accordance with Chapter III, Section 2 of the By-Laws it is provided that "Any twenty members may forward to the Secretary other nominations for any or all offices. All such nominations reaching the secretary at least sixty days before the Annual Meeting shall be printed, together with the names of the nominators, as special tickets."

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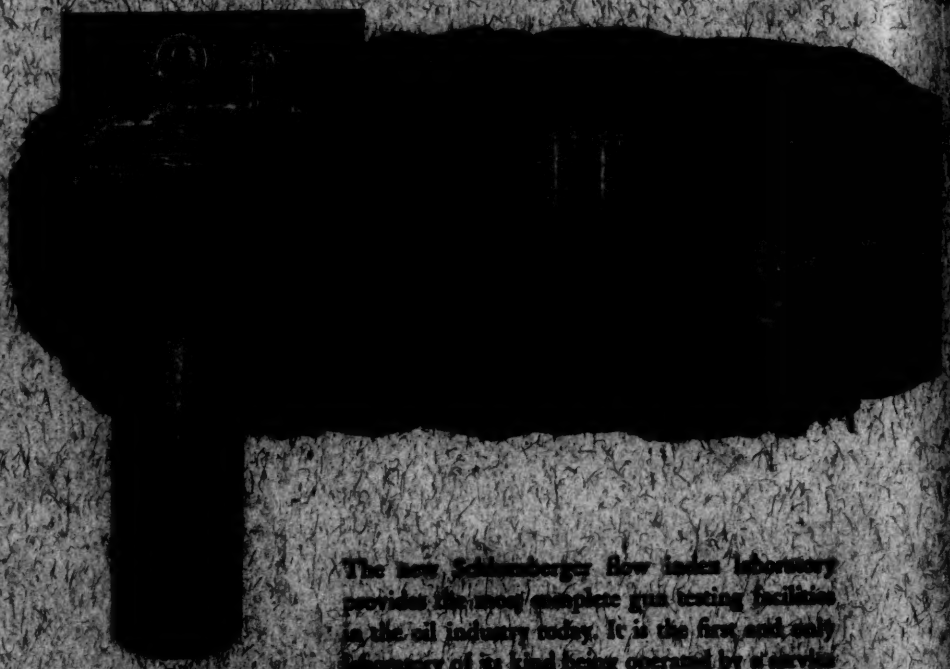

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